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TAXONOMY AND BIOLOGY OF THE NEARCTIC SPECIES OF HOMONEURA (DIPTERA: LAUXANIIDAE)* II. SUBGENUS HOMONEURA**

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Homoneura (Homoneura) van der Wulp, 1891

Malloch (1927c) was the first to use the subgenus *Homoneura* for the type, *picea*, and 4 closely related oriental species. The subgenus contains the bulk of the species of *Homoneura, s. lat.* This diverse assemblage of species probably can be subdivided into many groups, which may eventually be elevated to subgenera or distinct genera.

Diagnosis *Homoneura, s. str.*, can be distinguished from the other subgenera by the following combination of characters: (1) costal setulae ending abruptly at apices of R_{4+5}, (2) M_{1+2} not curved forward at apices, (3) 0 ia, (4) T2 without row of p bristles, (5) 2nd TS3 segments not darkened.

Discussion Nearctic *Homoneura, s. str.*, lack uniformly clouded marginal cells, possess 0+3 dc or 1+3 dc, and have 2 or 3 apical T2 spurs.

Key to Groups and Ungrouped Species of the Subgenus *Homoneura*

1. Wing maculated, apical and preapical spots occasionally rudimentary, represented by dark areas on the veins with faint bordering on adjacent membrane 2
   Wing immaculate, without indications of apical and preapical spots, or, at most, crossveins (r-m and m) darkened and faintly bordered 10
2. R_{4+5} with 2, occasionally 3, spots between r-m and apex (Figs. 43-47) 3
   R_{4+5} with at most 1 spot on this section (Figs. 42, 48-54, 56) 5
3. Preapical av F3 bristles present; parafacials ⅓rd width of face at middle; 0+3 dc . . . . *fraterna* group, p. 179 [key to 3 spp., p. 179]
   Preapical av F3 bristles absent; parafacials ½ width of face at middle; usually 1+3 dc 4
4. Arista long pubescent (Fig. 69); at most a weak presutural dc, close to suture; preapical d T3 slightly longer than width of T3 at its insertion [♂ with 2 large, ovate, heavily setulated appendages on venter of abdomen (fig. 93)] . . . . *lamellata*, p. 184
   Arista short plumose (Fig. 70); 1 strong presutural dc, well-removed anteriorly from suture; preapical d T3 shorter to subequal width of T3 at its insertion (Fig. 85) . . . . *occidentalis* group, p. 185 [key to 2 spp., p. 186]
5. R_{4+5} with 1 preapical spot about midway between r-m and apex; apical spots distinct (Figs. 42, 48-51, 53) 7
   R_{4+5} without any spot on this section; apical spots usually weak (Figs. 52, 54, 56) 6

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6. Presutural dc verv strong, well removed anteriorly from suture .... *shewelli*, p. 208
[see *setitibia* group, p. 207]
Presutural dc at most weak, close to suture .... *wheeleri*, p. 222
[see *aequalis* group, p. 220]
7. Gena ¼th height of eye; L3 trochanter with many dense setae (Fig. 86) .... *trochantera*, p. 206
[see *trochantera* group, p. 206]
Gena 1/6th height of eye; L3 trochanter with only sparse setae 8
8. Presutural dc weak; acr weak; arista long pubescent (Fig. 68) .... *conjuncta*, p. 188
Presutural dc absent or strong; acr strong, about size of prsc (Fig. 4); arista plumose (Fig. 72). 9
9. 1+3 dc, presutural dc strong; 4 rows acr .... *philadelphica*, p. 189
0+3 dc, 2 rows acr .... *incerta* group, p. 192
[key to 3 spp., p. 192]
10. 2 or 4 acr rows, inner rows weak to strong bristles; 3rd antennal segment unicolorous (Figs. 67-77) 11
6 acr rows of setae; 3rd antennal segment slightly browned apically (Fig. 78) .. *unguiculata*, p. 196
11. Crossveins r-m and m broadly bordered (Fig. 58); gena 1/6th height of eye. *nubila* group, p. 197
[key to 3 spp., p. 197]
Crossveins r-m and m at most darkened, with adjacent membrane faintly clouded; gena at most 1/5th height of eye 12
12. Frons distinctly swollen; parafacials approximately 2/3rds width of face at middle 13
Frons at most slightly swollen; parafacials usually at most ½ width of face at middle 14
13. Arista short pubescent (Fig. 67); 2 apical T2 spurs; L3 trochanter with numerous black setulae ventrally [black setulae also on basal ½ of F3 in ♂ (Fig. 83) and several on dorsum of cercus in ♀ (Fig. 106)] .... *littoralis*, p. 200
Arista long pubescent (Figs. 74-75); usually 3-4 apical T2 spurs; L3 trochanter with only sparse setae [anterior T2 claw of ♂ recurved, longer than posterior claw (Figs. 81, 82)] .... *harti* group, p. 201
[key to 3 spp., p. 201]
14. Parafacial ½ or greater than ½ width of face at middle 15
Parafacial less than ½ width of face at middle [facial ridge absent] 21
15. A slight, broad ridge present on ventral ⅓rd of face; 5th TS3 segments usually brown dorsally (Fig. 88) 20
Facial ridge absent; 5th TS3 segments yellow 16
16. av F1 ctenidium of 3-5 indistinct, very weak setulae .... *bakeri*, p. 204
avF1 ctenidium of 6-20 usually distinct, well-developed setulae (Figs. 79, 80) 17
17. L3 trochanter with dense setulae ventrally (Fig. 84) [usually weaker in ♀] 18
L3 trochanter with, at most, distinct dark setae ventrally 19
18. Arista short pubescent (Fig. 73) .... *inaequalis*, p. 204
Arista plumose (Fig. 77) .... *setula*, p. 205
19. r-m and m lightly bordered (Fig. 57); L3 trochanter with distinct black setae ventrally (Fig. 86); preapical T3 subequal to width of T3 .... *californica*, p. 207
[see *trochantera* group, p. 206]
wings immaculate (Fig. 63); L3 trochanter with only sparse setae; preapical T3 longer than width of T3 at its insertion .... *setitibia* group, p. 207
[key to 4 spp., p. 208]
20. r-m and m at most slightly darkened (Fig. 64); gena ¼th height of eye ..... *tenuispina*, p. 211
[pl corners of T6 with group of black bristles in ♂ (Fig. 117); small, black, oval cercus in ♀ (Fig. 118)]
r-m and m usually lightly bordered (Figs. 60, 62); gena ⅓rd height of eye. *bispina* group, p. 212
[small, black, flattened cercus in ♀ (Fig. 124)]
[key to 5 spp., p. 213]
21. r-m and m at most slightly darkened (Fig. 9); 5th TS3 segment yellow; presutural dc strong, well removed anteriorly from suture .... *cilifera*, p. 219
[♀ unknown]
r-m and m lightly bordered (Figs. 7, 61); 5th TS3 dark dorsally; presutural dc usually not well developed and close to suture .... *aequalis* group, p. 220
[key to 7 spp., p. 220]

Homoneura fraterna Group

Many early North American collection records belonging to this group were named *notata* Fallen, a Palaearctic species. The 1st record involved 2 specimens collected in Wisconsin by Thure Kumlien (van der Wulp, 1867). These specimens, at the Museum in Leiden, were too fragile to be sent for examination (Helsdingen, pers. com.). The collection records referring to *notata* could also belong to *lamellata*.

Diagnosis. This group of 3, medium-sized species possesses the following combination of characters: (1) distinct central and preapical spots in addition to the apical spots (Fig. 46); (2) presutural dc absent; (3) strong preapical av and ad F3 bristles present; (4) parafacials ⅓rd the width of face at middle; (5) preapical T3 bristle subequal to width of T3 at its insertion.

Discussion This group is similar to the *occidentalis* group in having distinct central and preapical spots, gena about 1/5th height of eye, and arista short plumose. In addition to these diagnostic characters, however, the *fraterna* group differs in having strong acr bristles, 5th TS2 and TS3 segments brown dorsally, and males with well-developed gonopods and terminal processes, with pl S5 processes absent.

The males of *birdi, fraterna*, and *pernotata* can be separated by differences in the genitalia. Females of *pernotata* can usually be separated from the other 2 species by reason of the heavily sclerotized S9. Females of *birdi* and *fraterna* cannot be separated with confidence at this time.

Key to Species of *fraterna* Group

1. Anterior angle of surstylus with a large, outer, ventrally directed spine, without an inner spine at posterior angle (Fig. 91); S9 of female mostly sclerotized (Fig. 92) *pernotata*, p. 179
   Anterior angle of surstylus with an outer lobe, bearing several small spines and a large, inner, ventrally directed spine at posterior angle (Figs. 89, 90); S9 of female with a few sclerotized areas 2
2. Male terminal processes with 2 posteriorly directed arms (Fig. 89) .... *fraterna*, p. 181
   Male terminal processes with 2 posteriorly directed arms and 1 ventrally directed arm (Fig. 90) .... *birdi*, p. 183

Homoneura (Homoneura) pernotata (Malloch)
(Figs. 91, 92)

Sapromyza pernotata Malloch, 1920: 128 [descr. - IL]. Malloch & McAtee, 1924: 20 [key]; Pl. 2, Fig. 24 [inferior forceps, ♂], Fig. 26 [genitalia, ♂].
Johannsen, 1926: 159 [coll. rec. - NY, several as *fraterna*, MISIDENT.].
Criddle, 1928: 100 [coll. rec. - MAN, = *fraterna*, MISIDENT.].
Johannsen, 1928: 848 [coll. rec. - NY, same as Johannsen, 1926].
Bird, 1930: 404, 440 [adult ecology - MAN, = *birdi*, MISIDENT.].
Shewell, 1938: 133 [key], 140 [coll. rec. - QUE, ONT, MAN, BC]; 138 (pl. 14) Fig. 57 [wing].
Ouellet, 1941: 135 [coll. rec. - QUE, some *fraterna* and *birdi*].
Chagnon, 1952: 29 [coll. rec. - QUE].
Shewell, 1965: 699 [cat., distr. - s. SASK to NS, s. to WI, IL and NY].

Diagnosis *H. pernotata* is easily separated from *birdi* and *fraterna* by differences in genitalia: surstylus with only an outer, ventrally directed spine and S9 of female usually highly sclerotized.

Discussion Males of *birdi* and *fraterna* have an inner, ventrally directed spine at the posterior angle of the surstylus (Figs. 89, 90), absent in *pernotata*, and terminal processes without an arm at right angles. The female S8 is broadly triangular, almost twice as wide as S10, and S9 is usually heavily sclerotized (Fig. 92). Females of *birdi* and *fraterna* possess a triangular S8, about as wide as S10, and only certain areas of S9 and S10 are sclerotized.

Types Holotype: ♂, Cedar Lake, [Lake County], Illinois, VIII-4-1906, tamarack gr. [bog] (INHS). Paratype: ♂, same data as holotype (INHS).

Specimens examined 174 (83♂, 91♀) from 76 north central and northeastern NA localities:
ALTA—1♂, Grand Prairie, VII-25-1961, A. R. Brooks (CNC).
CT—2♂, 3♀, 3 localities (AMNH).
IL—1♂, 3♀, Antioch, VIII-1-1930, Frison, Knight & Ross (INHS); 1 , IL, Belfrage (NRS); types.

MA—1♂, 1♀, Petersham, VII-30-1926, A. L. Melander (USNM).
MAN—4♂, 6♀, 5 localities (CNC).
ME—2♀, Orono, VII-27-, VIII-17-1958 (USNM).
MI—6♂, 8♀, 11 localities (CNC, CU, IASU, OHSU, SEM, UMI).
MN—11♂, 12♀, 9 localities (UMN).
MT—1♂, 3♀, 3 localities (KSU).
NH—2♂, 1♀, 3 localities (INHS, UNH, USNM).
NJ—1♂, Ramsey, VI-8-1921 (AMNH); 2 ˙, Ramsey, VI-21-1941, W. J. Gertsch (AMNH).
NS—1♂, 3♀, Kentville, VIII-6-1958, J. R. Vockeroth (CNC).
NY—5♂, 4♀, 6 localities (AMNH, CAS, CU, UMN, USNM).
OH—16♂, 12♀, 4.5 mi e. Kent, reared 1967-1969, R. M. Miller, biological note nos. 6723, 6724, 6823.5, 6824, 6825, 6828.5, 6924, 6925 (CNC, KSU, RMM).
ONT—9♂, 9♀, 11 localities (AMNH, CNC, IASU).
PA—2♂, 2 localities (PADA, SEM).
QUE—6♂, 16♀, 8 localities (CNC, UM)
SASK—3♂, Kenosee Lake, VIII-18-1955, C. D. Miller, A. R. Brooks (CNC).
WI—6♂, 8♀,5 localities (AMNH, NRS, SEM, UWI).

Remarks Shewell (1938) also reported this species from British Columbia.

Biology The flight period for this widespread and fairly common species begins at the end of May and extends through October, with the species most commonly collected in the months of July and August. Adults have been recorded from the following habitats: tamarack bogs, flood plain communities near tamarack bogs, alder-birch and poplar-birch associes, in a marsh, seep area at 1,524 m, and from forest floors. Shewell (1938) reported taking this species by sweeping basswood *(Tilia americana)* and *Spiraea*. Several of the examined specimens have been collected from Malaise traps.

Most rearings of *pernotata* were initiated by using adults collected from a stand of skunk cabbage *(Symplocarpus foetidus)* growing in a lowland deciduous woods at Renocera Marsh 7.2 km east of Kent, Ohio. Several rearings also were initiated by using adults reared from larvae collected in late winter and early spring from decaying leaves of sugar maple (*Acer saccharum*) and alder (*Alnus* sp.).

Field-collected males lives 23-73 days in the laboratory; females, 31-134 days. Reared males (8) lived 47-121 days; females (7), 36-127 days. The premating period for 2 reared females was 10 and 25 days with oviposition beginning 6 and 2 days later, respectively. Mating was observed twice in nature and in the laboratory and occurred in the morning or late afternoon and evening. The male was situated dorsally and faced in the same direction as the female, with his head near the midpoint of the female's thorax. The male's foretarsal claws were hooked on the sutural ridge between the notopleuron and mesopleuron, just anterior to the posterior np bristle of the female. His midtarsal claws were hooked on the costal margin of the female's wing base. The hindtarsi were appressed on the female's half-outstretched wings or were placed on the sides of her abdomen. The male seemed to use his hindtarsi to balance himself on the female's wings, but kept slipping. He used hopping movements to maintain the copulatory position. When the male's hindtarsi were appressed to the sides of the female's abdomen, the female's wings were held upright, while his were held together. Intermittently he released the grasp of his hindtarsi and then made quick hitting motions on the sides of her abdomen. The foretarsi were also released periodically and quick taps were made on her thorax. The fore and hindtarsi alternated in this slapping motion. Occasionally the female used her hindtarsi to agitate the male's genitalia. The pair remained in one place, except if greatly disturbed. Mating lasted 45 and 60 minutes in the laboratory.

The preoviposition period for 10 reared females ranged from 16-40 days. In the breeding jars, eggs were usually deposited singly on and in moist peat moss and underneath and between decaying tree leaves in the late afternoon and early evening. Field-collected females laid 165-582 eggs each, averaging 4-10 eggs daily. Reared females deposited 101-303 eggs each, averaging 4-6 eggs daily. The incubation period was usually 3-16 days, although some individuals required more time. Larvae mined and fed on decaying lettuce and tree leaves of maple and alder. The larval stadia were highly variable, and the extended periods required for development resulted in high mortality in the rearing dishes. Second instars were collected in the field from January through the beginning of April, when 3rd instars were found exclusively. In the laboratory rearing dishes of decaying leaves, 2nd instars molted to 3rd instars in 2-5 days. The 3rd-instar stadia ranged from 11-18 days, except those collected in mid-April, which molted in 5-6 days. For the completely laboratory-reared adults, the total larval period ranged from 44-101 days. The prepupal period was approximately 48 hours and pupal period was 10-14 days.

The total time required to complete a life cycle in the laboratory varied from 86-124 days, indicating that in northeastern Ohio this species is at least partially bivoltine. In nature, probably most eclosion takes place in the autumn, with the overwintering stages as quiescent, 1st-instar larvae. Development accelerates in early spring, with puparia being formed in May.

B. A. Foote (pers. com.) collected 2 gravid females in late June from herbage of a coniferous-deciduous woods, with the litter of *Populus trichocarpa* (western balsam poplar) abundant on the forest floor, at the University of Montana Biological Station 32.2 km east of Big Fork, Montana. Some larvae hatched and fed for a short time on rotting lettuce, but no pupae were obtained.

Homoneura (Homoneura) fraterna (Loew)
(Fig. 89)

Sapromyza fraterna Loew, 1861: 347 (Cent. 1, no. 77) [descr. - PA].
- Osten Sacken, 1878: 196 [cat., distr. - PA].
- Smith, 1890: 399 [coll. rec. - NJ].
- Townsend, 1892: 302 [key, distr. - PA].
- Lynch Arribalzaga, 1893: 262 [key], 293-294 [descr., after Loew, 1861].
- Johnson, 1900: 689 [coll. rec. - NJ].
- Aldrich, 1905: 585 [cat., distr. - PA, NJ].
- Cockerell, 1905: 251 [coll. rec. - NM, probably = *arizonensis*].
- Johnson, 1910: 798 [coll. rec. - NJ].
- Cole, 1912: 156 [coll. rec. - CA, = *occidentalis*, MISIDENT.].
- Gibson, 1912: 106 [coll. rec. - QUE].
- Melander, 1913: 68 [key, distr. - Europe, NH, NY, PA, NJ, CA, WA; Europe distr. refers to *notata*, CA & WA distr. refer to *occidentalis*].
- Walker, 1913: 395 [coll. rec. - ONT].
- Winn & Beaulieu, 1915: 152 [coll. rec. - ONT].
- Britton, 1920: 202 [coll. rec. - CT].
- Malloch & McAtee, 1924: 20 [key], 23 [coll. rec. - VA, MD]; Pl. 2, Fig. 18 [genitalia, ♂], Fig. 20 [inferior forceps, ♂], Fig. 21 [genitalia, ♂, ventral view].
- Johnson, 1925a: 254 [coll. rec. - ME, NH, VT, MA, RI, CT].
- Weese, 1925: 23, 24, 31 [adult ecology - IL].
- Criddle, 1926: 104 [coll. rec. - ONT].
- Johannsen, 1926: 159 [coll. rec. - NY, some = *pernotata*, MISIDENT.].
- Johnson, 1927: 216 [coll. rec. - ME].
- Criddle, 1928: 100 [coll. rec. - MAN, = *birdi* & *pernotata*, MISIDENT.].
- Johannsen, 1928: 848 [coll. rec. - NY, some = *pernotata*, MISIDENT.].
- Procter, 1938: 344 [coll. rec., same as Johnson, 1927].
- Shewell, 1938: 133 [key], 139 [coll. rec. - ONT, QUE].
- Procter, 1946: 398 [coll. rec., same as Johnson, 1927].
- Steyskal, 1947: 72 [distr. - TN, ONT, QUE, MAN, entire New England, NY, NJ, PA, VA, MD, MI, IL, CA, WA; CA & WA distr. refer to *occidentalis*].
- Shewell, 1965: 698 [cat., distr. - s. MAN to s. QUE, s. to KS and NC].

Diagnosis The anterior angle of the surstylus of *fraterna* and *birdi* lacks the outer, ventrally directed spine, present in *pernotata*, but has an outer lobe and a slightly curved, ventrally directed, inner spine at its posterior angle (Figs. 89, 90, 91). The terminal process in *fraterna* has 2 arms; in *birdi* it has 3. Females of *pernotata* have a highly sclerotized S9; those of *fraterna* and *birdi* appear to be very similarly lightly sclerotized.

Discussion The outer lobe of the surstylus in *fraterna* has a medially directed spine at its anterior angle, no spines ventrally, and a very strong, medially directed spine at its posterior angle. The outer lobe in *birdi* usually has small, medially directed spines at its anterior, ventral, and posterior angles. The terminal processes in *fraterna* have 2 tapering, posteriorly directed arms and no ventrally directed arm, whereas *birdi* has 1 long, narrow, ventrally directed arm and 1 large and 1 small, narrow, posteriorly directed arms. The aedeagus lacks lateral, basal spines characteristic of *pernotata* and *birdi* (Fig. 91c).

Types Lectotype: ♂, Pennsylvania, C. R. Osten Sacken, Loew coll. (MCZ 1681). Allolectotype: ♀, same data as lectotype (MCZ 1681).

Remarks I designated the male syntype as the lectotype and female as the allolectotype.

Specimens examined 139 (85♂, 54♀) from 55 north-central and northeastern NA localities:

CT—4♂, 2♀, 2 localities (USNM).

IA—15♂, 5♀, 7 localities (IASU); 1♂, 2♀, Woodman Hollow St. Pk., Webster Co., reared 1972, R. M. Miller (RMM); 3♂, 3♀, Red Haw St. Pk., 1 mi se. Chariton, reared 1975, R. M. Miller (RMM).

IL—1♂, 3♀, Elizabeth, VII-7-1917 (INHS); 3♂, 19♀, Urbana, VII-20-1920, C. P. A., cottonwood (INHS).

KY—1♂, TWL, Jefferson Co., VI-8-1954, P. J. Christian (LIM). 4♂, Lake Cumberland St. Pk., Russell Co., VIII-20-1962, D. L. Deonier, taken at forest edge (IASU).

MA—1♂, Brookline, Suffolk Co., VII-4, C. W. Johnson (MCZ).

MAN—3♂, 1♀, 3 localities (CNC).

MD—2♂, 2 localities (USNM).

MI—1♂, 1♀, N. Manitou Is., VIII-3-1957, R. E. Beer (SEM).

MN—5♂, 3♀, 4 localities (IASU, UMN).

NY—5♂, 3♀, 4 localities (CM, CU).

OH—1♂, 1♀, Kent State University Woods, Kent, reared 1969, R. M. Miller (RMM).

ONT—6♂, 1♀, 6 localities (CNC, USNM).

PA—1♂, South Gibson, Susq. Co., VIII-6-8-1917, J. C. Bradley (CU); 1 , PA, Belfrage (NRS).

QUE—16♂, 7♀, 8 localities (CNC,UM).

VA—3♂, 3 localities (CNC, IASU, USNM).

WI—5♂, 1♀, 5 localities (UWI).

WV—1♂, 2♀, Cheat Mts. (CM); 2 , Cranberry Glades, Pocahontas Co., VII-16-1955, W. W. Wirth, C. W. Sabrosky (USNM).

Remarks Because this species is widely distributed, most of the collection records, even the isolated female captures and records of *H. notata*, probably refer correctly to *fraterna*. Johnson (1925a) reported this species from Rhode Island, and I have seen females that are probably *fraterna* from all the New England states. Shewell (1965) recorded the southern limit of distribution of *fraterna* as North Carolina, from whence I have seen only females, and Kansas, but I have not seen specimens from this state. Steyskal (1947) collected this species in Tennessee, but I have seen only 1 female from that state. I have also recorded 1 female from South Dakota (IASU) and 1 from Idaho (SEM). I designated the male syntype as the lectotype and the female as the allolectotype.

Biology The flight period for this common species begins in mid-May and extends through September, with the species most commonly collected in the months of July and August. Adults have been recorded from the following habitats: forest edge, forest floor, near a tamarack bog, spruce-sand community from burr oak, powerline scrub, moist ash woods, oak forest, and cottonwoods. One specimen examined was collected from a Malaise trap. Weese (1925) recorded this species as fairly abundant throughout the study period of June 1 to September 1 in the herb stratum of an elm-maple forest in Illinois. Whittaker (1952) collected 1 female [unpublished] from the herb and shrub-low tree stratum in a gray beech forest in Tennessee.

At the end of January, 1969, 1 2nd-instar larva of *fraterna* was discovered among the wet, fallen leaves of the Kent State University Woods, Kent, Ohio. Sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and choke cherry (*Prunus viginiana*) were common near an old tamarack bog. A male emerged at the end of February. The prepupal period was approximately 48 hours; the pupal period, 13 days. Another 2nd instar was collected from the same site at the beginning of April, 1969. A female emerged in mid-May.

Eggs deposited by a female collected in August, 1972, at Woodman Hollow State Park, Iowa, were used to initiate a laboratory rearing. Most larvae hatched and fed on decaying lettuce and tree leaves. First and 2nd instars were still found in the rearing dishes in early October. One 2nd instar molted in 15 days, and 11 days later pupariated. The prepupal period was approximately 48 hours. Three adults emerged in mid-November, with the pupal periods lasting 14 and 15 days.

At the end of March, 1975, a number of 2nd and 3rd instars were collected among the fallen leaves of a lowland woods at Red Haw State Park, Iowa. The larvae were feeding mainly on decaying leaves of sugar maple. Two males and 3 females emerged at the beginning of May. The preoviposition period for 1 female was 20 days. This species probably has 1 generation per year, with the early larval instars as the overwintering stage.

Homoneura (Homoneura) birdi NEW SPECIES
(Figs. 46, 76, 90)

Gibson, 1918: 120 [coll. rec. - MAN, as *notata*, MISIDENT.].
Criddle, 1928: 100 [coll. rec. - MAN, as *fraterna*, MISIDENT.].
Bird, 1930: 404, 440 [adult ecology - MAN, as *pernotata*, MISIDENT.].

Diagnosis The anterior angle of the surstyli of *birdi* and *fraterna* lacks the outer, ventrally directed spin of *pernotata*, but has an outer lobe and a slightly curved, ventrally directed, inner spine at its posterior angle (Figs. 89-91). The terminal processes of *birdi* have 3 arms; those of *fraterna* have only 2. Females of *pernotata* have a highly sclerotized S9, whereas those of *birdi* and *fraterna* appear to be similar and lightly sclerotized.

Discussion The outer lobe of the surstylus of *birdi* shows considerable variation in shape and in combinations of small, medially directed spines at its anterior, ventral, and posterior angles. The outer lobe of *fraterna* has a medially directed spine at its anterior angle and a very strong, medially directed spine at its posterior angle, but lacks ventral spines. The terminal processes of *birdi* have 1 long, narrow, ventrally directed arm, subequal to 1 long, narrow, posteriorly directed arm and 1 smaller, narrow, posteriorly directed arm immediately dorsad of the longer posterior arm (Fig. 90b). The terminal processes of *fraterna* have 2 tapering, posteriorly directed arms and no ventrally directed arm (Fig. 89b). The aedeagi of *birdi* and *pernotata* have a pair of mediolateral spines, absent in *fraterna*.

From a long series collected at Bay's Branch Area, Iowa, variation in the outer lobe of the surstyli is very similar to variation in *fraterna*, and the terminal processes are similar to those of *birdi* (Fig. 90c). On the basis of the similarity in terminal processes and not being able to separate reliably the females of the variation—*birdi* or *fraterna*—I have included this variation in *birdi*. Specimens with this variation also are somewhat larger, approximately 3.5 mm whereas Canadian material is smaller, approximately 3 mm.

Description Total length 2.75-3.5 mm; wing length 3.2-3.7 mm. Yellow, with sparse, whitish pollinosity laterally and ventrally. Similar to *fraterna* and *pernotata*.

Head almost 1.5 times higher than long. Frons flat in profile, slight angle with facial plane; por equal distance between aor and iv. Face slightly convex; parafacials about ⅔rds width of face at middle. Gena about 1/5th height of eye. Arista short plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt slightly shorter than aor.

Thoracic chaetotaxy: 0 + 3 dc, acr bristle-like, in 2 regular rows. Legs yellow, except dorsal surface of apical tarsomeres of L2 and L3 brown. F1 av ctenidium with 11-13 closely spaced setulae; F3 with 1 strong preapical av bristle. Wing yellowish with 7 brown spots: r-m, m, apical R_{2+3}, central and preapical and apical R_{4+5}, and apical M_{1+2}.

Abdomen subshining. Male: T7 slightly longer than T6; surstylus and terminal processes as described; gonopods very long; aedegus large, with a pair of mediolateral spines; cercus moderately long, yellow, with slightly longer bristles apically. Female: anterolateral corners of S9 and S10 with rounded sclerotized areas; cercus yellow, with long bristles.

Types Holotype: ♂, Aweme, Manitoba, VIII-5-1924, R. D. Bird (CNC 15410). Paratypes: 1♂, 1♀, Birtle, Manitoba, VIII-6-1928, R. D. Bird (AMNH); 3♂, 3♀, North Branch, Ontario, VII-18-1960, S. M. Clark (CNC).

Remarks This species is named in honor of Ralph D. Bird for his contributions to the early study of biotic communities.

Specimens examined 110 (59♂, 51) from 24 north-central NA localities:

IA—28♂, 29♀, 4 localities (CNC, IASU); 5♂, 9♀, Bay's Branch Area, Guthrie Co., reared 1972-1973, R. M. Miller (CNC, RMM).
MAN—6♂, 5♀, 5 localities (CNC); ♂, holotype; 1♂, 1♀, paratypes.
MN—8♂, 1♀, 8 localities (UMN).
ONT—3♂, 1♀, 3 localities (CNC); 3♂, 3♀, paratypes.
QUE—3♂, 2♀, 2 localities (UM).
VA—1♂, Clator Lake St. Pk., Pulaski Co., VI-12-1971, W. H. Robinson (USNM).

Biology The flight period of this rather uncommon species extends from June through August, with most collection records in the months of July and August. The species has been collected from the following habitats: basswood-maple, poplar-birch associes, and a floodplain community near a tamarack bog.

Bird (1930) collected this species [as "*pernolata*"] from the treetop, shrub, and herb strata of a mature poplar (*Populus tremuloides*) stand in the Aspen Parkland of central Canada. This species was one of the more abundant insects in the tree-top collections. I have examined several specimens collected by Bird and all have proved to be *birdi*, although the records may be mixed because females were collected and *fraterna* and *pernotata* also occur in Manitoba.

In June, 1972, some rearings of the variation *birdi* were initiated by using adults collected in a small, lowland stand of cottonwood (*Populus deltoides*), black cherry (*Prunus serotina*), and silver maple (*Acer saccharinum*) in the middle of a cornfield at Bay's Branch Area, Iowa. The females of 1 rearing deposited many eggs on the decaying lettuce and leaves provided as larval substrate. Not until September 1, however, were 1st instars noted. Second instars were observed the beginning of October and 3rd instars by the end of October. Two adults from a 2nd rearing emerged in October, 3 from the 1st rearing in November, 1 in February, and 1 in March.

Field-collected males lived 38-54 days in the laboratory; females, 40-56 days. Reared males (2) lived 32-67 days; females (3), 35-66 days. The premating period for 1 reared female was 13 days, and oviposition began that afternoon. One mating was observed briefly one morning and was very similar to that of *pernotata*. Preoviposition period for the 3 reared females was 13-25 days. In late afternoon and early evening, eggs were laid singly on the peat moss and decaying leaves. One reared female laid 210 eggs, averaging 5 eggs daily.

At the end of May, 1973, a number of additional larvae were collected from the decaying leaves at Bay's Branch Area. The larvae fed on the decaying black cherry and silver maple leaves. The prepupal period was approximately 48 hours, with the pupal period for males ranging from 10-11 days and females, 11-12 days. Two males and 5 females emerged from June 8 to June 23.

From the laboratory and field information, it seems that this species is univoltine with quiescent larvae as the overwintering stage.

Homoneura lamellata incertae sedis

Homoneura (Homoneura) lamellata (Becker)
(Figs. 44, 69, 93)

Sapromyza lamellata Becker, 1895: 204 [descr. - Polen.; type locality = POLAND, not Russia].
Slosson, 1895b: 320 [coll. rec. - NH, as *notata*, MISIDENT.].
McGillivray [Macgillivray], 1903: 13 [coll. rec. - NY, as *notata*, MISIDENT.].
Sapromyzosoma deceptor Malloch *in* Malloch & McAtee, 1924: 20 [key], 24 [descr. - NH].
Johnson, 1925a: 255 [coll. rec. - ME, NH, MA].
Johnson, 1927: 216 [coll. rec. - ME].
Bird, 1930: 404, 440 [adult ecology - MAN].
lamellata Czerny, 1932: 15-16 [redescr., distr. - n. Austria, Russia], Fig. 14 [genitalia, ♂, ventral view].
deceptor, Procter, 1938: 344 [coll. rec. - ME, same as Johnson, 1927].
Homoneura armata Shewell, 1939: 264-265 [descr. - ALTA].
cactifera Shewell, 1940: 86 [n. name for *armata* Shewell, preocc. Malloch, 1925: 320].
deceptor Procter, 1946: 398 [coll. rec. - ME, same as Johnson, 1927].
armata Strickland, 1946: 166 [coll. rec. - ALTA].
lamellata Shewell, 1965: 698 [cat., distr. - YT to e. QUE, s. to MA, Holarctic; *deceptor* Malloch, *armata* Shewell, *cactifera* Shewell, synonyms].
Cole, 1969: 373 [distr. - ALTA].
Shtakel'berg, 1970: 201 [key, distr. - central w. Europe].
Shewell, 1971: 8 [note, distr. - Mongolia, Russia, n. Austria, CAN, ne. USA].
Remm, 1972: 122 [adult ecology - Estonia, Finland, Leningrad region].

Diagnosis This species is related to the Nearctic *fraterna* and *occidentalis* groups but differs from both by possessing only a weak preapical av F3 bristle and from the *occidentalis* group by the arista being pubescent (Fig. 69) rather than short plumose (Fig. 70). *H. lamellata* is also closely related to the Palaearctic *notata* Fallen, both species having the same wing pattern and chaetotaxy, except *notata* has the apical spots somewhat more distinct, arista short plumose, and 5-7 stout, preapical, pv F3 bristles in males.

Discussion Males of *lamellata* are easily recognized by the rather large, elongate-oval, ventral plates (lamellae) arising on the pl corners of T5 and S5 (Fig. 93), which are strongly setulose apically.

H. lamellata has at most a weakly developed presutural dc, close to the suture and about ½ the anterior postsutural dc, whereas the *fraterna* group lacks a presutural dc and the *occidentalis* group has a very strong presutural dc, well removed anteriorly from the suture and about the same size as the anterior postsutural dc. *H. lamellata* also has a higher frequency of an additional central spot occurring between the r-m and preapical and apical R_{4-5} spots (Fig. 44). This condition usually occurs in only 1 wing, the other showing the normal maculation.

Type Holotype:♂, Polen., J. Schnabl coll. (ZMHU).

Remarks The type locality is Poland, not Russia as Becker's (1895) description stated (Schumann, pers. com.). According to Becker's description and Czerny's (1932) redescription, there was also supposed to be a female (allotype) that is now evidently lost, although there is another male from Schnabl's collection at the Zoological Museum of Natural Science, Humboldt University, Berlin. Several specimens from the Zoological Museum, Helsinki, were also compared with Nearctic material.

Specimens examined 172 (74♂, 98♀) from 67 northern NA localities:

AK—1♂, 2♀, 3 localities (KSU, USNM).
ALTA—8♂, 15♀, 8 localities (CNC, KSU, UALTA); ♂, holotype [*armata*] (CNC 4902); ♀, allotype [*armata*] (CNC 4902).
BC—13♂, 13♀, 11 localities (AMNH, CNC).
CO—1♀ Estes Pk., VII-11-1934, A. L. Melander (USNM).
ID—1♂, Kootenai Co., 12 mi n. Coeur d'Alene, VII-1-1959, G. W. Byers (SEM).
MAN—2♂, 1♀, 3 localities (CNC).
ME—1♂, Mt. Katahdin, VII-4-1968, D. M. Wood (CNC).
MI—4♂, 2♀, 5 localities (CNC, UMI, USNM).
MN—1♀, Eaglesnest, VI-14-1959, W. V. Balduf (INHS).
MT—1♀, 9 mi n. Swan Lake, VII-19-1964, K. Valley (KSU).
NH—1♂, 1♀, Benton, VII-6-1931, A. L. Melander (USNM); 1♀, White Mts., [H. K.] Morrison (ZMHU 7586); ♀, holotype [*deceptor*] (USNM 26390); 1♀, paratype [*deceptor*] (USNM).
NY—1♀, Adirondack Mts., Axton, VII-12-22-1891, A. D. MacGillivray & C. O. Houghton (CU).
ONT—7♂, 4♀, 6 localities (CAS, CNC).
QUE—3♂, 5♀, 6 localities (CAS, UM).
SASK—26♂, 44♀, 8 localities (CNC).
SD—1♂, 3♀, 3 localities (SDSU, USNM).
WI—1♂, Rusk Co., T35N R7W B30, VI-15-1953, light trap, R. H. Roberts (UWI).
YT—4♂, 3 localities (CNC).

Remarks Johnson (1925a) also reported this species from Massachusetts, and the specimens in H. K. Morrison's collection marked "White Mts." were mostly taken on Mt. Washington, New Hampshire. Slosson (1895b) reported *notata*, which most likely was *lamellata*, taken in the alpine region or above 1,675 m on the summit of Mt. Washington.

Biology This widespread, fairly common species has been collected most frequently in June and July, during the flight period from late May through late August. Remm (1972) reported the flight period beginning in early June and extending through early August in the Soviet Baltic Republics. She also reported the species to be rare and found in damp forests. On the other hand, Shewell (1971) stated that *lamellata* seems to be commoner in the prairies and has been taken in numbers in thickets of aspen (*Populus*) in southern Saskatchewan. Bird (1930) collected a male in the tree-top stratum of a mature poplar stand in southern Manitoba. Specimens examined included several collected from 671 to 792 m in elevation in British Columbia and 1 each, from a light trap, Malaise trap, and on *Epilobium* (common fireweed).

Homoneura occidentalis Group

Early western collection records referring to *notata* and *fraterna* belong to this group, and probably to the more common *occidentalis*.

Diagnosis The 2 small species of this group can be distinguished by the following combination of characters: (1) 1 strong presutural dc present; (2) a short preapical d T3 bristle present; (3) distinct central, preapical, and apical spots, except M_{1+2} weak (Figs. 43, 47); (4) parafacials ½ width of face at middle; (5) preapical av and ad F3 bristles absent.

Discussion This group is also distinguishable from the *fraterna* group by having tarsi yellow and males with p1 S5&6 processes.

Key to Species of *occidentalis* Group

1. Preapical d T3 bristle usually greater than ½ diameter of T3 at its insertion; aedeagus rounded apically .... *arizonensis*, p.187
   Preapical d T3 bristle no more than ½ diameter of T3 at point of its insertion; aedeagus pointed apically (Fig. 85) .... *occidentalis*, p.186

Homoneura (Homoneura) occidentalis (Malloch)
(Figs. 45, 47, 85, 94)

Baker, 1904: 32 [coll. rec. - CA, NV, as *notata*, MISIDENT.].
Cole, 1912: 156 [coll. rec. - CA, as *fraterna*, MISIDENT.].
Melander, 1913: 68 [key, distr. - CA, WA, as *fraterna*].
Woodworth, 1913: 137 [insect guide - CA, as *notata*].
Sapromyza occidentalis Malloch, 1920: 127 [descr. - CA].
Malloch & McAtee, 1924: 20 [key].
Sapromyzosoma nudifemur Malloch *in* Malloch & McAtee, 1924: 21 [key], 24 [descr. - BC; *Sapromyzama*, as found in some reprints, error]. NEW SYNONYMY.
Criddle, 1926: 104 [coll. rec. - BC].
Knowlton, Harmston & Stains, 1939: 11 [coll. rec. - UT, = *knowltoni*, MISIDENT.].
occidentalis Knowlton, Harmston & Stains, 1939: 11 [coll. rec. - UT, = *arizonensis*, MISIDENT.].
Steyskal, 1947: 72 [distr. - CA, WA, as *fraterna*].
nudifemur Foxlee, 1957: 37 [coll. rec. - BC].
Shewell, 1965: 699 [cat., distr. - s. BC; as var. of *occidentalis*].
occidentalis Shewell, 1965: 699 [cat., distr. - CA, s. BC, UT, AZ, NM].
nudifemur Cole, 1969: 373 [distr. - BC].
occidentalis Cole, 1969: 373]distr. - BC to CA, e. to UT and NM].

Diagnosis This species differs from *lamellata* and the *fraterna* group by the presence of a very strong presutural dc bristle. *H. occidentalis* can be separated from the closely related *arizonensis* by possessing a very small preapical d T3 bristle, which is no more than ½ the diameter of T3 at its point of insertion and at most only slightly longer than the suberect T3 setae (Fig. 85).

Discussion Identification of this species is sometimes difficult because of variation in the wing spot pigmentation, which is similar to the situation found in *H. wheeleri*. Some spots are represented by darkened areas on the veins or only faint membrane clouding in the positions corresponding to the normal spot development (Fig. 47). These individuals may be teneral specimens, whereas others have the normal brown spots (Fig. 45).

Specimens without any obvious wing spots caused Malloch & McAtee (1924) to describe the species *nudifemur*. In his description Malloch mentioned the presence of a dark part on the 3rd vein (R_{4+5}) beyond the outer crossvein (m). Shewell (1965) suspected the possible synonymy and lowered *nudifemur* to varietal status.

Males of *occidentalis* can be readily distinguished from *arizonensis* by the apex of the aedeagus being distinctly narrowed and pointed rather than broadly pointed (Figs. 94, 95). Also, the bifid p1 S5&6 process has its larger posterior extension bluntly pointed rather than rounded. The dorsal and posteroventral setae of the male cercus are subequal, whereas *arizonensis* has much longer setae apically.

Types Lectotype: ♂, Pasadena, California, J. M. Aldrich (USNM 26253). Allolectotype: ♀, same data as lectotype (USNM). Paralectotypes: 4♂, same data as lectotype (USNM); 1♂, Laguna Beach, southern California, C. F. Baker (USNM).

Remarks The holotype of this species is presumed lost, and the remaining 7 specimens mentioned by Malloch (1920) were all labeled as paratypes. Therefore, I have considered these specimens as a syntype series of equal status and have designated 1 male as the lectotype and the sole female as the allolectotype.

Specimens examined 297 (210♂, 87♀) from 77 western NA localities:

AZ—1♂, Santa Maria, VI-22-1940, E. D. Ball (USNM).

BC—1♂, 1♀, Robson, VII-26-1947, H. R. Foxlee (CNC); ♂, holotype [*nudifemur*] (USNM 40876); 1♂, paratype [*nudifemur*] (USNM).

CA—178♂, 68♀, 62 localities (AMNH, CAS, CDA, CM, CNC, CU, LACM, MCZ, OHSU, OKSU, PC, SEM, UCAB, UCAD, UCAR, USNM, UTXA, WASU); types.

ID—3♂, 4♀, Moscow, VII-24-1925, C. L. Fox (CAS); 2♂, 25 mi e. Boise, Ada Co., VII-6-1968, A. R. G. Hins, sweeping alongside Cinch Creek (UID).

OR—1♂, Corvallis, VII-5-1965, D. J. Borror (OHSU); 1♂, Grande Ronde River, N. Imbler, Union Co., VII-19-1936, G. Ferguson (CU).

UT—11♂, 10♀, 5 localities (CNC, UTSU).

WA—3♂, 3♀, 4 localities (USNM, WASU).

Remarks Baker (1904) reported *notata* from the mountains near Claremont, California, and in Ormsby County, Nevada. I have seen many of Baker's specimens from Claremont, and all have proved to be *occidentalis*. I have not examined any specimens from Nevada, but suspect that they are also *occidentalis*. Likewise, Cole's (1912) collection record of *fraterna* belongs to *occidentalis*, because this is the only spotted species that I have seen from Laguna Beach, California.

Biology This species is very common in California, and its flight period begins at the end of April and extends through the end of October, with the adults being most common during June, July, and August. Some adults have been recorded from *Salix* (willow), Shamel ash (*Fraxinus* sp.), peach (*Prunus persica*), avocado (*Persea* sp.), *Grindelia camporum* (tarweed), *Physalis ixocarpa* (ground cherry), and *Helianthus annuus* (common sunflower). Specimens examined also included 2 taken in Malaise traps and at light.

Homoneura (Homoneura) arizonensis NEW SPECIES
(Figs. 43, 70, 95)

Cockerell, 1905: 251 [coll. rec. - NM, as *notata*, MISIDENT.].
Knowlton, Harmston & Stains, 1939: 11 [coll. rec. - UT, as *occidentalis*, MISIDENT.].

Diagnosis This species differs from *lamellata* and the *fraterna* group by the presence of a very strong presutural dc bristle. *H. arizonensis* can be separated from the closely related *occidentalis* by having the preapical d T3 bristle greater than ½ the diameter of T3 at the point of its insertion and distinctly longer than the appressed T3 setae.

Discussion This species is generally slightly smaller than *occidentalis*. All specimens that I have examined have well-developed maculations (Fig. 43). Males can be readily distinguished from *occidentalis* by the apex of the aedeagus being rounded rather than pointed (Figs. 94, 95). Also the pl S5&6 process has its larger posterior extension broadly rounded rather than pointed. The posteroventral setae of the males' cerci are twice as long as the dorsal setae, while these setae are subequal to the dorsal ones in *occidentalis*.

Description Total length 2.75-3.25 mm; wing length 3-3.5 mm. Brownish-yellow with whitish pollinosity laterally and ventrally. Similar to *occidentalis*.

Frons flat in profile, rounded into facial plane; por placed slightly closer to iv than aor. Face flat; parafacials about ½ width of face at middle. Gena about 1/5th height of eye. Arista short plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong and well in front of suture; acr weak bristles, in 2 regular rows.

Legs with av F1 ctenidium with 7-9 closely spaced setulae; F3 without preapical av, pv or ad bristles. T3 with small preapical d bristle, longer than ½ width of T3 at point of its insertion and longer than appressed T3 setae.

Wings with r-m, m, apical R_{2+3}, central and preapical R_{4+5}, apical R_{4+5}, and weak apical M_{1+2} spots.

Abdomen of male with T6 twice the length of T5; S2 about 3 times as large as S3; S5&6 bifid, with larger posterior processes rounded; aedeagus rounded apically; surstylus foot-shaped, toe directed posteriorly; cercus with posteroventral setae twice as long as dorsal setae.

Types Holotype: ♂, Southwestern Research Station, 5 mi sw. Portal, Arizona, V-23-VI-5-1967. 1646 m, Malaise trap, C. W. Sabrosky (USNM 75371). Allotype: ♀, same locality as holotype, VI-1967, black light, C. W. Sabrosky (USNM). Paratypes: 2♂, same data as holotype (USNM); 1♂, same locality as holotype, IX-5-25-1965, C. W. Sabrosky, Malaise trap (USNM); 1♂, same locality as holotype, VI-5-9-1972, W. W. Wirth, Malaise trap (USNM); 1♀, same locality as holotype, VI-22-1950, O. L. Cartwright, sweeping (USNM); 5♂, 4♀, same locality as holotype, V-22-1965, V. Roth, Malaise trap (CAS, UCAR); 4♂, 2♀, Big Bend National Park, Oak Spring, Texas, V-1-1959, J. F. McAlpine, 1372 m (CNC).

Specimens examined 89 (32♂, 57♀) from 27 southwestern USA localities:

AZ—5♂, 7♀, 6 localities (CNC, SEM, UAZ, UTXA); holotype, allotype, paratypes (USNM).

CA—1♂, Darwin Falls, 4 mi w. Panamint Springs, Inyo Co., VII-13-1962, J. A. Litsinger (UWI); 2♀, Blythe, V-1-1955, W. R. Richards (CNC); 4♀, Andreas Can., 0[sic]-20-1951, A. H. Sturtevant (USNM); 2♀, Morongo, IX-26-1944, A. L. Melander (USNM).

NM—4♂, 13♀, 5 localities (CNC, USNM, UTXA).

TX—4♂, 2♀, paratypes.

UT—8♂, 14♀, 11 localities (CNC, UTSU).

Biology The flight period for this rather uncommon species ranges from early May to late September. Adults have been collected at elevations of 1,372 and 1,646 m. Specimens examined included 1 collected at black light and many taken in Malaise traps. One specimen was collected on apricot *(Prunus armeniaca)*.

Homoneura conjuncta incertae sedis

Homoneura (Homoneura) conjuncta (Johnson)
(Figs. 42, 68, 100)

Sapromyza conjuncta Johnson, 1914: 22-23 [descr. - RI, MA, VT, NJ].
Weiss, 1915: 107 [coll. rec. - NJ].
Headlee, 1916: 484 [coll. rec. - NJ].
Malloch & McAtee, 1924: 21 [key], 23 [coll. rec. - DC, VA]; Pl. 2, Fig. 22 [genitalia, ♂; = *H. (Tarsohomoneura)* sp.?].
Johnson, 1925a: 255 [coll. rec. - VT, MA, RI].
Hallock & Parker, 1926: 18 [coll. rec. - NY].
Johannsen, 1926: 159 [coll. rec. - NY].
Johannsen, 1928: 848 [coll. rec. - NY].
Smith, 1928: 491 [adult ecology - IL].
Shewell, 1938: 135 [key], 139 [note, coll. rec. - QUE, ONT]; 134 (Pl. 12), Fig. 35 [genitalia, ♂], 138 (Pl. 14), Fig. 61 [wing].
Shewell, 1965: 698 [cat., distr. - s. ONT & QUE, s. to IL & SC].

Diagnosis This small species has apical R_{2-3}, preapical and apical R_{4-5}, apical M_{1-2} spots and bordered r-m and m. *H. conjuncta* also has a weak presutural dc and arista long pubescent.

Discussion This species is related to the subgenus *Tarsohomoneura* in lacking preapical av F3 bristles and having a wing pattern similar to *americana* and *johnsoni* with the apical R_{2-3} and preapical R_{4-5} spots usually fused (Figs. 39, 41, 42). However, *conjuncta* lacks the black TS3 segments, possesses acr row of weak bristles and different terminal processes.

The male genitalia of *conjuncta* are small and similar to *citreifrons*, although *conjuncta* lacks surstylar extensions and has foot-shaped terminal processes (Fig. 100). *H. citreifrons* has broad, lobed surstyli and arm-shaped terminal processes (Fig. 24).

Malloch & McAtee (1924: pl. 2, Fig. 22) presented a figure of a male hypopygium that is not *conjuncta*. Shewell (1938) suggested that 2 closely related species may be involved, but I have not seen any specimens with genitalia that match the figure. However, the many long spines, which usually are not extended, at the tip of the aedeagus are characteristic of aedeagi in the subgenus *Tarsohomoneura* (Fig. 29). *H. conjuncta* has only some short, broad spines within the aedeagus (Fig. 100).

Types Holotype: ♂, Buttonwood, Rhode Island, VI-18-1912, C. W. Johnson (MCZ 7875). Paratypes: 1♂, Auburndale, Massachusetts, VIII-2, C. W. Johnson (MCZ); 1♂, 1♀, Manomet, Massachusetts, VII-26-27-1905, C. W. Johnson (USNM, MCZ); 1♀, Jamesburg, New Jersey, VII-4-1894 (MCZ); 1♀, Avalon, New Jersey, VI-8 (USNM); 1♂, Amsdem, Vermont, VII-10-1908 (MCZ).

Remarks According to Johnson's (1914) list of the paratypes, there should be 1 more from Blue Hill, Massachusetts, which I could not locate.

Specimens examined 125 (49♂, 76♀) from 67 eastern NA localities:

DC—1♀, Washington, V-20-1912, D. W. Coquillett (USNM).

IA—1♀, Spring Brook Lake St. Pk., Guthrie Co., VI-9-1973, R. M. Miller (IASU); 1♀, Ledges St. Pk., Boone Co., V-31-1950, J. L. Laffoon (IASU).

IL—4♂, 13♀, 9 localities (INHS, USNM, UTXA).

IN—1♂, Lafayette, VII-4-1914, A. L. Melander (USNM).

MA—3♀, 3 localities (MCZ, USNM); 2♂, 1♀, 2 localities, paratypes.

MD—1♂, Laurel, V-26-1965, Malaise trap (CNC).

MN—4♂, 2♀, 5 localities (IASU, UMN).

NJ—2♀, Vineland, VII-1954, M. R. Wheeler (UTXA); 2♀, 2 localities, paratypes.

NY—1♂, 6♀, 5 localities (CAS, CU, NYSM).

OH—7♂, 7♀, 7 localities (KSU, MOU, OHSU).

ONT—12♂, 16♀, 7 localities (CNC).

PA—7♂, 7♀, 4 localities (ANSP, CM, USNM).

QUE—3♂, 5♀, 5 localities (CNC, UM).

RI—♂, holotype.

SC—2♂, Aiken, VI-13-1957, J. R. Vockeroth (CNC).

VA—2♂, 5♀, 4 localities (IASU, MCZ, USNM).

VT—1♂, paratype.

WI—1♂, 2♀, 3 localities (UWI).

WV—1♀, Cranberry Glades, Pocahontas Co., VII-16-1955, C. W. Sabrosky (USNM).

Biology The flight period for this commonly collected species extends from early May to late August, with collection records indicating that *conjuncta* is more common in June and July. One adult has been associated with cottonwood *(Populus deltoides)* and a number with red osier *(Cornus stolonifera)* and Juneberry *(Amelanchier)*. Smith (1928) classified *conjuncta* as a seasonal sub-influent (noticeably affects community by their abundance during part of the year) in the vernal society (April 26 to May 29) of 2 red oak-maple climax forests in Champaign County, Illinois.

Homoneura philadelphica incertae sedis

Homoneura (Homoneura) philadelphica (Macquart)
(Figs. 3, 4, 53, 80, 96)

Sapromyza philadelphica Macquart, 1843: 348 (1843: 191) [descr. - NA].

Walker, 1849: 987 [coll. rec. - GA, = *fuscibasis*, MISIDENT.; NS, = *americana*, MISIDENT.].

Osten Sacken, 1858: 77 [cat., distr. - GA, NS].

Walker, 1871: 144 [coll. rec. - NS, = *americana*, MISIDENT.].

Osten Sacken, 1878: 196 [cat., distr. - Atlantic states].

Brodie & White, 1883: 56 [coll. rec. - CAN].

van der Wulp, 1883: 56 [coll. rec. - QUE, = *incerta*, MISIDENT.].

Keen, 1885: 55 [coll. rec. - PA].

Smith, 1890: 399 [coll. rec. - NJ].

Townsend, 1892: 302 [key, distr. - NA].

Lynch Arribálzaga, 1893: 261 [key], 286-287 [note, descr. after Macquart].

Slosson, 1895a: 7 [coll. rec. - NH].

Harrington, 1900: 134 [coll. rec. - ONT].

Johnson, 1900: 689 [coll. rec. - NJ].

Aldrich, 1905: 586 [cat., distr. - Atlantic states, QUE, NH, NJ].

Crevecoeur, 1906: 95 [coll. rec. - KS].

Washburn, 1906: 81 [coll. rec. - MN].

Johnson, 1910: 798 [coll. rec. - NJ].

Melander, 1913: 68 [key, distr. - QUE, NH, MA, NJ, PA, LA, IL, SD].

Shelford, 1913: 239, 257 [note on ecology - IL].

Winn & Beaulieu, 1915: 152 [coll. rec. - QUE].

Britton, 1920: 202 [coll. rec. - CT].

Malloch & McAtee, 1924: 21 [key], 23 [distr. - MD], Pl. 2, Fig. 19 [genitalia, ♂].

Johnson, 1925a: 255 [coll. rec. - ME, NH, VT, MA, CT].

Johnson, 1925b: 96 [coll. rec. - NH].

Weese, 1925: 31 [adult ecology - IL].
Criddle, 1926: 104 [coll. rec. - QUE].
Johannsen, 1926: 159 [coll. rec. - NY].
Johnson, 1927: 216 [coll. rec. - ME].
Johannsen, 1928: 848 [coll. rec. - NY].
Smith, 1928: 491, 494 [adult ecology - IL].
Petch & Maltais, 1932: 65 [coll. rec. - QUE].
Smith-Davidson, 1932: 310, 326 [adult ecology - IL].
Curran, 1934: 316, Fig. 4 [wing].
Brimley, 1938: 380 [coll. rec. - NC].
Procter, 1938: 344 [coll. rec. - ME, same as Johnson, 1927].
Shewell, 1938: 135 [key], 140 [coll. rec. - QUE, ONT; note]; 134 (Pl. 12) Fig. 40a, 40b [genitalia, ♂], 136 (Pl. 13) Fig. 58 [wing].
Osborn & Knull, 1939: 256 [coll. rec. - OH].
Procter, 1946: 399 [coll. rec. - ME, same as Johnson, 1927].
Shelford, 1951: 189 [adult ecology - IL].
Shewell, 1965: 699 [cat., distr. - SD & s. MAN to se. CAN & ME, s. to LA & GA].
Shewell, 1966: 213 [note on aristae].

Diagnosis This medium-sized species is readily recognized by having apical R_{2+3}, preapical and apical R_{4+5}, apical M_{1+2} spots, and bordered r-m and m (Fig. 53). It also has 1+3 dc, a strong preapical av F3 bristle, and plumose arista.

Discussion This species is related to the *incerta* group, having similar maculation and with the base of R_{4+5} infuscated as in *fuscibasis* (Fig. 49, 53). *H. philadelphica* is easily separated by the strong presutural dc and only short, pointed surstylus (Fig. 96-99). Some specimens have 1-4 marginal setae between the dc bristles (Fig. 4), rather than these areas usually being devoid of setae.

Shewell (1938: 134, Figs. 40a, 40b) figured and discussed some of the variations in the inferior forceps (= terminal processes). As far as I have been able to determine, these are individual variations that I could not correlate with the presence or absence of marginal setae on the scutellum or any other character. Most specimens do not have extra setae; the forms having them seem to occur where large numbers of the species are present. I have collected and reared many specimens, with and without the marginal scutellar setae, from Renocera Marsh, 7.2 km east of Kent, Ohio, and have also examined several specimens from Ontario, Minnesota, and New York.

Shewell (1966) noted that *philadelphica* is the only Nearctic species in which the plumosity of the arista approaches the length found in the introduced oriental species, *H. unguiculata*. However, the plumosity of the aristae of *fuscibasis* and *crickettae* is as long as in *philadelphica*.

Redescription Total length 3.5-4 mm; wing length 3.5-4.7 mm. Brownish-yellow, with very sparse whitish pollinosity. Similar to *fuscibasis*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face flat; parafacials about ⅓ width of face at middle. Gena about 1/6th height of eye. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong, shorter than succeeding dc, not far removed anteriorly from suture; 1+4 acr, as strong as prsc, with 2 incomplete outer rows of setae. F1 av ctenidium of 12-15 closely spaced setulae; F3 with strong preapical ad and av and without pv bristles. Wings yellowish with both r-m and m bordered brown; apical R_{2+3}, preapical and apical R_{4+5}, and apical M_{1+2} spots brown; base of R_{4+5} infuscated.

Male genitalia: surstylus short and bluntly pointed on a1 angle; gonopods moderately long and curved posteriorly; terminal processes vary slightly, but basically club-shaped, with approximately 6 minute setulae apically; aedeagus moderately large; cercus medium-sized, with some longer bristles apically.

Type Neotype: ♂, Philadelphia, Pennsylvania, VII-20-1893, C. W. Johnson (MCZ 32306).

Remarks The location of Macquart's type is unknown and presumed lost. It is not in the Museum National d'Histoire Naturelle, Paris (Tsacas, pers. com.). The earliest collected male from Philadelphia was selected as the neotype.

Specimens examined 1209 (588♂, 621♀) from 296 central and eastern localities:

AR—1♂, Washington Co., VIII-12-1965, E. P. Rouse (UAR).
CT—9♂, 12♀, 9 localities (AMNH, CU, IASU, MCA, USNM).
GA—20♂, 22♀, 4 localities (ANSP, CNC, CU, MNW, SEM, USNM).

IA—103♂, 72♀, 21 localities (IASU, USNM); 15♂, 9♀, 4 localities, reared 1971-1975, R. M. Miller (RMM).
IL—28♂, 34♀21 localities (AMNH, ANSP, CAS, INHS, NRS, PC, USNM, UTXA).
IN—8♂, 2♀, 5 localities (FSCA, IASU, PU, USNM).
KS—1♀, Onaga, Crevecoeur (USNM).
KY—2♂, Lexington, VII-27, VIII-7-1894, H. Garman (UKY).
LA—1♂, Opelousas, IV-1897 (USNM).
MA—9♂, 1♀, 4 localities (IRSNB, USNM).
MAN—9♂, 4♀, 4 localities (CNC).
MD—4♂, 5♀, 5 localities (CM, CNC, USNM).
ME—10♂, 21♀, 6 localities (CU, MCZ, OHSU, USNM).
MI—12♂, 12♀, 12 localities (CU, SEM, UMI, USNM).
MN—19♂, 13♀, 15 localities (ANSP, IASU, NCSU, UTXA).
MO—1♂, Atherton, VIII (USNM).
NC—6♂, 5♀, 5 localities (AMNH, CNC, IASU, NCSU, UTXA).
ND—1♀, Trail Co., VIII-14-1923, A. A. Nichol (UMN).
NH—5♂, 7♀, 6 localities (AMNH, UNH, USNM, ZMHU).
NJ—13♂, 16♀, 9 localities (AMNH, ANSP, BMNH, CM, CU, INHS, MCZ, USNM).
NS—1♀, Kentville, VIII-6-1958, J. R. Vockeroth (CNC).
NY—60♂, 61♀, 28 localities (AMNH, BMNH, CAS, CM, CNC, CU, MCZ, NYSM, UMN, USNM).
OH—44♂, 44♀, 15 localities (CNC, CU, FSCA, KSU, OHSU, UMN); 47♂, 55♀, 4.5 mi e. Kent, reared 1967-1969, R. M. Miller, biological note nos. 6721-22, 6820-22, 6920-33 (CNC, RMM).
ONT—33♂, 33♀, 23 localities (AMNH, BMNH, CAS, CNC, CU, MNW, USNM).
PA—56♂, 78♀, 36 localities (ANSP, CM, CSU, CU, FEM, MCZ, PADA, PC, SEM, USNM, ZMHU); ♂ type.
QUE—36♂, 68♀, 19 localities (AMNH, CNC, UALTA, UM).
SD—1♂, Waubay, VII-26-1924, H. C. Severin (SDSU).
TN—6♂, 8♀, 4 localities (CNC, CU, USNM).
VA—13♂, 17♀, 12 localities (CNC, IASU, INHS, MCZ, USNM, UTXA).
VT—3♀, 3 localities (MCZ, PU, USNM).
WI—11♂, 11♀, 12 localities (ANSP, IASU, SEM, UWI).
WV—5♂, 5♀, 4 localities (CM, INHS).

Biology The flight period of this very common and widespread species begins in early May and extends through late October, with most collection dates being from the summer months of June, July, and August. Several adults have been collected at lights, in light traps, at light during a heavy rain, and from elevations up to 2,012 m. Specimens have been recorded from *Populus deltoides* (cottonwood), *Tilia americana* (basswood), *Fraxinus nigra* (black ash), *Carya ovata* (shagbark hickory), *Taxus canadensis* (ground hemlock), and a species of Urticaceae (the nettle family).

Adults have also been associated with the following habitats: dry creek beds; along rivers, meadows, prairies, marshy ponds; powerline scrub; forest floors; near tamarack bogs; maple-elm floodplain community; oak-chestnut, alder-birch, poplar-birch, and spruce-yellow birch (*Betula lutea*) associations. Shelford (1913) recorded *philadelphica* as common in the field stratum of a white oak-red oak-hickory association and listed this species in the herbs of the beech-maple climax near Chicago, Illinois. Weese (1925) reported that this species was collected on June 26 from the herb stratum of an elm-maple forest near the University of Illinois, Urbana. Smith (1928) classified *philadelphica* as a seasonal influent (importantly affects community by their abundance during part of the year) in the estival society (May 29 to July 19) and as a seasonal subinfluent (noticeably affects community during part of the year) in the vernal (April 26 to May 29) and serotinal (July 19 to September 6) societies of 2 red oak-maple climax forests in Champaign County, Illinois. By using these same 2 red oak-maple climax forests, Smith-Davidson (1932) showed that this species responded to the variability in weather conditions by attaining its maximum abundance during the summer of 1926, which was much wetter than the summer of 1925. Shelford (1951) listed *philadelphica* along with *incerta* in his work on the fluctuations of forest animal populations in east central Illinois. Whittaker (1952) collected 5 specimens [unpublished] from late June to mid-July in Tennessee—1 from the sparse herb stratum of an eastern hemlock forest, 3 from the herb and shrub-low tree strata of a gray beech forest, and 1 from the shrub and herb strata of a cove forest of mixed deciduous trees in a ravine.

Several adults were reared from larvae collected from leaf litter, mostly decaying sugar maple leaves *(Acer saccharum)* from various locations around Iowa (Red Haw State Park, Pilot Mound State Forest, Ledges State Park, and Bay's Branch Area) from 1971 to 1975. Larvae were collected at the end of December, end of March, and middle of April and May. Adults reared from larvae collected in winter began emerging in mid-April in the laboratory; those from larvae collected in mid-April began emerging in mid-May; and the 1 collected in mid-May emerged in early June.

During 1967 to 1969, a few rearings of *philadelphica* were initiated by using adults collected in great abundance from a stand of skunk cabbage *(Symplocarpus foetidus)* growing in a lowland deciduous woods at Renocera Marsh, 7.2 km east of Kent, Ohio. A number of rearings were also initiated using adults reared from larvae collected in late winter and early spring from decaying leaves of sugar maple and alder *(Alnus)*.

Field-collected males lived 44-137 days in the laboratory; females, 54-110 days. Reared males lived 53-156 days; females, 55-141 days. The premating period for 7 reared females was 10-36 days with oviposition beginning about 2 days later. Mating was observed 6 times in the laboratory and occurred in late afternoon and evening. Mating position and behavior were similar to those described for *pernotata*. Mating lasted 2-4 hours.

The preoviposition period for reared females ranged from 12-42 days. In the breeding jars, eggs were usually deposited in clusters of 4-5 on and in moist peat moss and underneath and between decaying tree leaves in the late afternoon and early evening. Field-collected females laid up to 10 eggs each per day, which 1 reared female laid 13 eggs per day. The incubation period was usually 3-13 days, although some individuals required longer time. Larvae mined and fed on decaying lettuce and tree leaves of maple and alder. The larval stadia were 6-16 days for 1st instars, 3-13 for 2nd instars, and 9-20 for 3rd instars. First instars were collected in the field from January through mid-April; 2nd and 3rd instars were collected in late April and May. The prepupal period was approximately 48 hours; the pupal period was 10-13 days.

The total time required to complete a life cycle in the laboratory varied from 90-131 days, indicating that in northeastern Ohio this species is at least partially bivoltine. In nature most eclosion probably takes place in the autumn, with the overwintering stages as quiescent 1st-instar larvae. Development accelerates in early spring, with puparia being formed in May.

Homoneura incerta Group

Diagnosis This group of 3 species can be separated by the following combination of characters: (1) apical R_{2-3}, preapical and apical R_{4-5}, apical M_{1-2} spots, and bordered r-m and m; (2) 0+3 dc; (3) 2 rows of strong acr; (4) gena 1/6th height of eye; (5) parafacials ⅓rd width of face at middle.

Discussion This group is closely related to *philadelphica*, which obviously differs by the strong presutural dc bristle; otherwise, it could easily belong to the *incerta* group. Females of the *incerta* group can be very hard to distinguish especially when *incerta* females are large specimens and the apical R_{2-3} spots are not distinctly darker than the other spots. Presence of preapical av F3 bristles is variable as probably are the infuscated bases of the R_{4-5} in *fuscibasis* and *crickettae*.

Key to Species of *incerta* Group

1. Apical R_{2+3} spots much darker, more conspicuous and usually larger than other wing spots (Fig. 51); 1 strong presutural acr; small genitalia (Fig. 97) .... *incerta*, p. 192
   Apical R_{2-3} spots not more conspicuous or larger than others (Figs. 49, 50); 2 strong presutural acr; large genitalia (Figs. 98, 99) 2
2. Base of R_{4-5} usually infuscated; long, simple gonopods .... *fuscibasis*, p. 194
   Base of R_{4-5} not infuscated; bifurcate gonopods .... *crickettae*, p. 195

Homoneura (Homoneura) incerta (Malloch)
(Figs. 51, 72, 97)

van der Wulp, 1883: 56 [coll. rec. - QUE, as *philadelphica*, MISIDENT.].
Sapromyza incerta Malloch, 1914: 36-37 [descr. - MD, DC, IL].
Malloch & McAtee, 1924: 21 [key], 23 [coll. rec. - MD].
Johnson, 1925a: 255 [coll. rec. - MA].

Criddle, 1926: 104 [coll. rec. - QUE, ONT.].
Johannsen, 1926: 159 [coll. rec. - NY].
Johnson, 1927: 216 [coll. rec - ME].
Johannsen, 1928: 848 [coll. rec. - NY].
Petch & Maltais, 1932: 159 [coll. rec. - QUE].
Procter, 1938: 344 [coll. rec. - ME].
Shewell, 1938: 135 [key], 140 [coll. rec. - QUE, ONT]; 134 (Pl. 12) Fig. 42 [genitalia, ♂], 138 (Pl. 14) Fig. 56 [wing].
Jones, 1946: 186, 188 [adult ecology - IL].
Procter, 1946: 349 [coll. rec. - ME, same as Procter, 1938].
Dowdy, 1947: 432 [adult ecology - MO].
Shelford, 1951: 189, 191, 206 [adult ecology - IL].
Shewell, 1965: 698 [cat., distr. - s. MAN to se. CAN and NH, s. to MO and n. GA].

Diagnosis This small species can be recognized by its distinctly larger and darker apical R_{2+3} spot (Fig. 51). *H. incerta* can be separated from the larger *crickettae* and *fuscibasis* by having only 1 strong presutural acr.

Discussion This species is most closely related to *crickettae* and *fuscibasis* by having 3 strong postsutural dc, a strong preapical av F3 bristle and arista plumose (Fig. 72). Both *crickettae* and *fuscibasis* are usually larger than 3.5 mm, have 2 strong presutural acr, and all wing spots pigmented equally. The male genitalia of *incerta* have short, posteriorly hooked surstyli; moderately long, straight gonopods; long, somewhat foot-shaped terminal processes, crenulated dorsally; very long aedeagus and small cerci (Fig. 97).

Types Lectotype: ♀, Plummers Island, Maryland, VIII-10-1912, W. L. McAtee. Allolectotype: ♂, Washington, District of Columbia, IX-2-1907, W. L. McAtee (USNM) [left L3 & wings missing]. Paralectotypes: 2♀, same locality as lectotype, VIII-17-1912, W. L. McAtee (USNM); 1♀, Aldridge, Illinois, VIII-11-1891, C. A. Hart & Shiga [Acc. No. 17212] (INHS).

Remarks The 3 females from Plummers Island at the United States National Museum were all labeled cotypes. Therefore, I selected the female in the best condition and designated it the lectotype and the male allotype as the allolectotype. According to Malloch's (1914) description, there was supposed to be a male paratype at the Illinois National History Survey. Because Frison (1927) only listed the female from Aldridge, the male must be lost.

Specimens examined 434 (195♂, 239♀) from 191 north central and eastern NA localities:

CT—5♂, 5♀, 3 localities (USNM).
DC—2♂, 5♀, 2 localities (COSU, OHSU); ♂, allolectotype.
GA—4♂, 1♀, 2 localities (ANSP, CNC).
IA—10♂, 34♀, 7 localities (IASU); 1♂, Stone St. Pk., reared 1972, R. M. Miller (RMM); 2♂, 2♀, Red Haw St. Pk., reared 1974, 1975, R. M. Miller (RMM).
IL—2♂, 4♀, 4 localities (FMNH, INHS); 1♀, paralectotype.
IN—2♂, 3♀, 4 localities (PU, USNM).
KY—12♂, 1♀, Lake Cumberland St. Pk., Russell Co., VIII-20-1962, D. L. Deonier, taken at forest edge (IASU).
MA—9♂, 9♀, 9 localities (IRSNB, MCZ, MU, SEM, USNM).
MAN—2♂, 4♀, 2 localities (CNC).
MD—5♂, 7♀, 5 localities (ANSP, MCZ, USNM); ♀, lectotype; 2♀, paralectotypes.
ME—3♂, 5♀, 5 localities (CU, OHSU, USNM).
MI—8♂, 17♀, 12 localities (CNC, IASU, SEM, UMI).
MN—4♂, 6♀, 6 localities (IASU, UMN).
MO—1♂, 2♀, 3 localities (PU, USNM).
NC—3♂, 5♀, 4 localities (AMNH, CNC, FSCA, IASU).
NH—5♂, 3♀, 6 localities (CU, UNH, USNM, ZMHU).
NJ—1♀, Princeton, X-1, A. H. Sturtevant (USNM).
NS—1♀, Shelburne, VIII-10-1958, J. R. Vockeroth (CNC).
NY—18♂, 17♀, 21 localities (AMNH, CAS, CM, CU, IASU, NYSM, USNM).
OH—19♂, 7♀, 9 localities (FSCA, IASU, OHSU, UMN); 2♂, 3♀, Kent, reared 1968, 1972, R. M. Miller, B. A. Foote (RMM, KSU).
ONT—13♂, 11♀, 8 localities (AMNH, CAS, CNC, USNM).
PA—8♂, 14♀, 17 localities (ANSP, CM, CU, FEM, FSCA, IASU, PADA, USNM).

QUE—13♂, 26♀, 15 localities (AMNH, CNC, IRSNB, NRS, UALTA, UM).
SD—6♂, 1♀, Newton Hills St. Pk., Lincoln Co., VII-29-1967, S. Medina Gaud, J. L. Laffoon (IASU).
TN—5♂, 1♀, 5 localities (IASU).
VA—24♂, 23♀, 16 localities (CNC, FSCA, IASU, INHS, MCZ, SEM, USNM, UTXA, ZMH).
WI—5♂, 17♀, 15 localities (IASU, UWI).
WV—1♂, 1♀, 2 localities (CM).

Biology The flight period of this common species begins in early June and extends through late October, with most collection dates in July and August. Jones (1946) reported the dates of first and last appearances of *incerta* from the herbs in the William Trelease Woods, a maple-elm woodland, 7 km northeast of Urbana, Illinois: first appearance—May 8, 1934; May 24, 1935; June 14, 1937; June 5, 1938; last appearance—September 12, 1934; September 6, 1937. I suspect that the 1st records for May belong to *citreifrons*. Shelford (1951) also used this same woods in his study of animal population fluctuations. He concluded that *incerta* could be used for quantitative studies, but regular collections were too few to constitute good samples, identification difficulties caused gaps in the records, and this probably was the species that declined and disappeared about the middle of the sampling period.

Adults have been collected commonly at lights, many from light traps, and 1 each from a blacklight trap and a Malaise trap. Malloch & McAtee (1924) also reported that this species comes to light. Many adults were collected at the edge of a forest and several from a moist ash woods and a maple-elm floodplain community. Specimens have been recorded from *Fagus grandifolia* (beech), cottonwood *(Populus deltoides)*, honey locust *(Gleditsia triacanthos)*, American elm *(Ulmus americana)*, *Tilia americana* (basswood or linden), *Fraxinus nigra* (black ash), *Acer saccharum* (sugar maple), *Carya* sp. (hickory), and many species of *Quercus* (oaks). Dowdy (1947) collected a specimen of *incerta* in early July from the tree stratum of an oak-hickory forest near Jefferson City, Missouri. Whittaker (1952) collected 5 specimens [unpublished] from late June to mid-July in Tennessee—2 from the herb and shrub-low tree strata of a gray beech forest, 1 from the herb-low shrub and high shrub-low tree strata of a red oak-pignut hickory forest, 1 from a shrub community with a layer of heath, and 1 from the shrub and herb strata in an open stand of pines. One pair was taken *in copula* on August 4th (Ohio).

In mid-September, 1968, a rearing was initiated by using a field-collected female from a mesic woods in Kent, Ohio. She laid 222 eggs in 22 days in the laboratory. The eggs were deposited singly on leaves and peat moss in the early evening. The larvae fed on decaying maple and cherry leaves and on lettuce. In mid-November 1 male and in mid-December 2 females emerged. The preoviposition period was 24-26 days, but all eggs laid were evidently inviable. The male lived almost 2 months, 1 female a little more than 2 months, and the remaining female 5 months. Foote (pers. com.) reared 1 specimen from the decaying leaves of *Sassafras albidum* (white sassafras) on December 30, 1972, and another specimen from *Acer rubrum* (red maple) in the spring of 1973 at Kent, Ohio.

In early August, 1971, a rearing was initiated using field-collected females from an oak woods in Stone State Park, Sioux City, Iowa. The larvae fed on decaying leaves and lettuce, 1 male emerging in mid-November. Its 2nd-instar stadium lasted 9 days; 3rd, 20 days; and pupal period, 10 days. In mid-April, 1974, and mid-March, 1975, late instar larvae were collected from sugar maple leaves in a mesic woods at Red Haw State Park, 1 mi east of Chariton, Iowa. About 1 month later the adults began emerging.

From the biological information known about this species, I suspect that it has only 1 generation a year since it is more common in mid- to late summer. Probably the species overwinters as larvae.

Homoneura (Homoneura) fuscibasis (Malloch)
(Figs. 49, 98)

Walker, 1849: 987 [coll. rec. - GA; as *philadelphica*, MISIDENT.].
Sapromyza fuscibasis Malloch, 1920: 126 [descr. - IL, MD].
Malloch & McAtee, 1924: 21 [key], 23 [coll. rec. - VA, MD].
Brimley, 1938: 380 [coll. rec. - NC].
Shewell, 1965: 698 [cat., distr. - IL to sw. ONT & NJ, s. to MS & FL].

Diagnosis This large species is very similar to *crickettae* but has the base of the R_{4+5} infuscated, long, simple gonopods, flattened apically, but *crickettae* lacks the basal infuscation of R_{4+5} and has short, bifurcate gonopods apically (Figs. 49, 50, 98, 99).

Discussion This species has at least 2 very strong presutural acr, and preapical av F3 bristles may be present or absent. *H. crickettae* also has 2 strong presutural acr and usually possesses a strong preapical av F3 bristle. Some specimens of *fuscibasis* do not have distinct infuscations at the bases of the R_{4+5}, which makes females of *fuscibasis, crickettae,* and sometimes large specimens of *incerta* very difficult to identify.

Types Holotype: ♂, White Heath, Illinois, VII-11-1915, J. R. Malloch (INHS). Allotype: ♀, Summer, Illinois, VIII-2-1914, C. A. Hart (INHS). Paratypes: 2♂, same data as holotype (INHS, USNM); 1♂, 2♀, same data as allotype (CNC, INHS, USNM); 1♀, St. Joseph, Illinois, VI-27-1915 (INHS); 1♂, Dubois, Illinois, VIII-8-1917, J. R. Malloch (INHS); 1♂, Urbana, Illinois, IX-15-1891, J. Marten [Acc. No. 17499] (INHS); 2♀, Plummers Island, Maryland, VI-28, IX-13-1914, W. L. McAtee (USNM).

Specimens examined 81 (39♂, 42♀) from 50 eastern NA localities:

FL—5♀, 4 localities (FSCA, USNM).
GA—2♂, 1♀, 3 localities (BMNH, CNC, ZMHU).
IA—1♀, Ledges St. Pk., Boone Co., VIII-13-1971, W. L. Kramer (IASU); 2♂, 2♀, Red Haw St. Pk., reared 1975, R. M. Miller (RMM).
IL—4♂, 2♀, 4 localities (IASU, INHS, UTXA); holotype; allotype; 5♂, 3♀, paratypes.
IN—1♂, Lafayette, VII-4-1914, A. L. Melander (USNM).
KY—2♂, 1♀, Lexington, VIII-7-1894, H. Garman (UKY).
LA—2♂, 2♀, 2 localities (FMNH, OHSU).
MD—4♂, 1♀, 4 localities (OHSU, USNM); 2 , paratypes.
MO—1♂, St. Louis, VIII-12-1953, Stalker (UTXA); 1♀, Cuivre River St. Pk., Lincoln Co., VIII-26-1961, J. L. Laffoon (IASU).
MS—2♂, Oxford, V-1943 (USNM).
NC—1♂, 1♀, 2 localities (CAS, CNC).
NJ—3♂, 2♀, 4 localities (AMNH, CU, FEM, MCZ, UTXA).
NY—1♂, Montauk, Long Island, VI-9-1953, R. Latham (USNM); 1♂, Speonk, Long Island, VIII-12-1954, L. Wilcox (USNM).
OH—3♀, 2 localities (KSU, MCZ); 1♂, 4♀, 4.5 mi e. Kent, reared 1968, 1969, R. M. Miller (RMM).
ONT—1♂, 1♀, 2 localities (CAS, CNC).
QUE—1♂, 3♀, Ste-Anne Sorel, VII-26-1950, A. Robert (UM).
TN—2♂, 3♀, 3 localities (CNC)
VA—2♂, 3♀, 4 localities (IASU, MCZ, USNM).

Biology The flight period of this uncommon species begins in late April (Louisiana) and extends to mid-October (Florida). One adult has been collected from *Fagus grandifolia* (beech) and 1 at a light.

In the spring of 1968 and 1969, larvae were collected from the leaf litter, mostly *Acer rubrum* (red maple), at Renocera Marsh, 4.5 mi east of Kent, Ohio. Five adults emerged in the latter half of May. In late March, 1975, larvae were collected from decaying leaves of *Acer saccharum* (sugar maple) at Red Haw State Park, 1 mi east of Chariton, Iowa. Four adults emerged in the latter half of April. This species is probably univoltine, with larvae being the overwintering stage.

Homoneura (Homoneura) crickettae NEW SPECIES
(Figs. 50, 99)

Diagnosis This medium-sized species is very similar to *fuscibasis*, but lacks the infuscated base of the R_{4+5}; males have short, bifurcate gonopods.

Discussion This species has at least 2 very strong presutural acr, as does *fuscibasis*, and usually has a strong preapical av F3 bristle, which *fuscibasis* may or may not possess. Males of *crickettae* also have small, broadly pointed surstyli, but they are moderately long and mesally curved in *fuscibasis* (Figs. 98, 99). The terminal processes and aedeagi of both species are very similar. Females of *crickettae* can be easily confused with females of *fuscibasis* and sometimes large specimens of *incerta*.

Description Total length 3.5-4 mm; wing length 3.6-4 mm. Brownish-yellow, with very sparse whitish pollinosity. Similar to *fuscibasis*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face slightly convex; parafacials about ⅓rd width of face at middle. Gena about 1/6th height of eye. Arista plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 0+3 dc; 2+3 acr, presutural acr about as strong as prsc, with 2 outer rows of setae. F1 av ctenidium of 9-11 closely spaced setulae; F3 with preapical ad, with or without av, and without pv bristles. Wings yellowish with r-m and m bordered brown; apical R_{2+3}, preapical and apical R_{4+5} and apical M_{1+2} spots brown.

Male surstylus small, broadly pointed; terminal processes large, curving posteriorly, with small setulae apically; gonopods short, bifurcate at tip; aedeagus large; cercus medium-sized.

Types Holotype: ♂, Berks Co., No. 2 French Creek Park, Pennsylvania, VII-3-1958, G. W. Byers & party (SEM). Allotype: ♀, same data as holotype (SEM). Paratypes: 4♂, 1♀, same data as holotype (SEM, USNM); 2♂, 1♀, collection data unknown [2936, 2937, 2939], G. N. Hough (FMNH).

Remarks This species is named after my wife's nickname. The collection records for Hough's specimens have been lost (Kethley, pers. com.).

Biology Nothing is known about the biology of this rarely collected east-central species.

Homoneura unguiculata incertae sedis

Homoneura (Homoneura) unguiculata (Kertész)
(Figs. 78, 104)

Lauxania (Minettia) unguiculata Kertész, 1913: 100-101 [descr. - Formosa]; Fig. 3b [head], Figs. 3d, e, f, [genitalia, ♂].
Malloch, 1929a: 51 [key]; Pl. 6, Fig. 91 [genitalia, ♂].
Frost, 1964: 157 [coll. rec. - FL, as *Homoneura* sp.].
Frost, 1966: 250 [coll. rec. - FL, as *unguiculata*, ERROR].
Shewell, 1966: 212-213 [redescr. - FL, SC, introd.].

Diagnosis This small, clear-winged species can easily be separated from all other Nearctic *Homoneura* by its 6 rows of acr setae rather than 2 or 4 rows, and apex of the 3rd antennal segment light brown (Fig. 72) rather than unicolorous, yellow-orange. Also the plumosity of the arista is longer than that of any other Nearctic species.

Discussion Shewell (1966) in his redescription of *unguiculata* stated that the av F1 ctenidium is inconspicuous and sometimes absent. All the material that I have examined, however, possessed a ctenidium of 9-12 weak setulae.

The male genitalia are small and very different from other Neartic *Homoneura* (Fig. 104), possessing a characteristic shiny, light brown, recurved, claw-like surstylus. The cercus of the female is dark brown.

Types Lectotype: ♂, Takao, Formosa, VI-13-1907, [H.] Sauter (HNHM). Paralectotypes: 1♀, Takao, Formosa, III-24-1907, 300 m, Sauter (HNHM); 5♀, Takao, Formosa, VI-13-, VI-24-, XI-8-, XII-3-1907, Sauter (HNHM); 2♀, Yentempo, Formosa, V-19-1907, Sauter (HNHM); 1♂, 5♀, Koshun, Formosa, IX-, X-1908, I-1909, Sauter (HNHM); 3♂, 4♀, Tainan, Formosa, IV-, V-1912, Sauter (HNHM); 1♀, Taihoku, Formosa, IV-1912, Sauter (HNHM).

Remarks During transit many of the 23 syntypes were badly damaged. Of the 5 males and 18 females, only 1 male, which I designated as the lectotype, and 10 females remained in good condition. Specimens from Hawaii were also compared with Oriental and Nearctic material.

Specimens examined 68 (40♂, 28♀) from 26 southeastern USA localities:

AL—4♂, Kushla, V-20-1956, A. H. Sturtevant (LACM, USNM).
FL—18♂, 18♀, 16 localities (CNC, FEM, FSCA, IASU, KSU, USNM, WASU).
GA—2♂, 3♀, Stone Mt., DeKalb Co., XI-11-1953, Dodge (USNM).
NC—1♂, Mt. Pisgah, VII-17-1958, D. A. Young (NCSU); 1♀, Raleigh, IX-17-1961, H. D. Blocker (NCSU).
SC—15♂, 6♀, 6 localities (CNC, NCSU, USNM).

Remarks *H. unguiculata* is widespread in the Oriental region and has immigrated to Hawaii (Hardy, pers. com.). The earliest Nearctic record is April 14, 1952, from Elfers, Florida. Specimens were collected the following year in Georgia and 4 and 5 years later in South Carolina and North Carolina, respectively. Perhaps the species is migrating northward from Florida, but it seems as likely that this species has been in this general area for a number of years, with the collection records indicating where most of the active collecting has taken place.

Biology Since *unguiculata* is cosmopolitan, it is probably an opportunistic species that breeds in a wide variety of decaying plant materials. Adults have been collected in light traps, Steiner, Malaise and stickyboard traps, from sweeping weeds, at *Bidens pilosa* (a type of burmarigold), and from *Celtis laevigata* (a type of hackberry). Shewell (1966) reported that during intensive collecting at Highlands, North Carolina, *unguiculata* was taken only on the few excursions to elevations below 305 m. One of the paratypes was collected at 300m.

From the Nearctic collection records, the species seems to be fairly common in early spring and again in the fall. However, specimens have been collected in every month of the year in Florida, indicating that the species is probably multivoltine.

Homoneura nubila Group

Diagnosis This group of 3 large species has the following combination of characters: (1) r-m and m strongly bordered; (2) a strong preapical av and ad F3 bristle; (3) 1+3 dc, presutural dc strong and well-removed anteriorly from the suture; (4) gena 1/6th height of eye; (5) parafacials ⅓rd width of face at middle.

Discussion This group also has arista short plumose and 5th TS3 segment yellow. The males of the 3 species of this group can be separated by characters of the T3 and genitalia. Females of the 3 species cannot be distinguished at this time. Furthermore, it is not uncommon to collect more than 1 of these species in the same habitat.

Key to Species of *nubila* Group

1. ♂T3 with a fringe of long, fine, erect av bristles 2
   ♂T3 with only appressed setae [S5 with apical fringe of strong setae] . . . . *nubila*, p. 197
2. ♂L3 basitarsi with a fringe of long, fine, av bristles [S5 with apical fringe of black setulae] . . . . *nubilifera*, p. 198
   ♂L3 basitarsi with only short setae [S5 without any differentiated apical setae] *aldrichi*, p. 199

Homoneura (Homoneura) nubila (Melander)
(Fig. 101)

Minettia nubila Melander, 1913: 66 [key], 74 [descr. - IL, KS, OR; OR as var. = *setula*, MISIDENT.].
Malloch & McAtee, 1924: 21 [key], 23 [coll. rec. - VA].
Shewell, 1965: 699 [cat., distr. - IL, sw. ONT, KS, AR, NC, VA].

Diagnosis Males of *nubila* are separable from males of *nubilifera* and *aldrichi* by the absence of a fringe of long, fine, erect av T3 bristles and the presence of a foot-shaped surstylus.

Discussion The T3 and L3 basitarsi of males have only short setae and S5 has some larger setae, but not distinct setulae, as found in *nubilifera*. The surstyli and terminal processes of *nubila* are foot-shaped, with the toe of the former directed anteriorly and that of the latter directed posteriorly (Fig. 101).

Types Lectotype: ♀, Lawrence, Kansas, J. M. Aldrich (USNM 49927). Paralectotype: ♀, Chicago, Illinois, VIII-10-1901 (USNM).

Remarks Although I have not been able to distinguish the females of this group, I have selected the Kansas specimen as the lectotype because all the males that I have examined from that state are what has previously been called *nubila*. The Illinois specimen could be any 1 of the 3 species.

Specimens examined 129 (69♂, 60♀) from 41 central and eastern NA localities:

AR—1♂, Arkansas, VIII-10-1907 (UAR); 1♂, Howard Co., V-13-1935, W. F. Turner, swept from peach (USNM).

IA—15♂, 13♀, 3 localities (IASU); 1♂, 2♀, Bay's Branch Area, Guthrie Co., reared 1973, R. M. Miller; 1♂, Red Haw St. Pk., 1 mi e. Chariton, reared 1975, R. M. Miller (RMM).

IL—9♂, 4♀, 6 localities (INHS, USNM); 1♀, paralectotype.

IN—1♂, Dubois Co., VI-29-1937, Ferdinand (PU).

KS—23♂, 27♀, 10 localities (CM, CNC, IASU, KSSU, LIM, OHSU, USNM); 3♂, 7♀, 2 mi sw. Jennings, reared 1972, R. M. Miller (RMM); lectotype.

MO—1♂, 1♀, 2 localities (USNM); 6♂, 5♀, Blackjack, reared 1933, R. B. Swain, ex artichoke trash (CNC, USNM).
NE—1♂, Hershey, VIII-5-1972, R. M. Miller (IASU); 1♂, Lincoln, VI-13-1903, W. D. Pierce (UNE).
OK—3♂, 3 localities (OKSU).
ONT—1♂, 1♀, Pt. Pelee, IX-8-9-1954, G. S. Walley (CNC).
VA—1♂, Arlington, VII-8-1936, J. R. Malloch (USNM).

Remarks Shewell (1965) reported this species from North Carolina, but I have seen only 1 female (USNM) from there. I have also seen 1 female from Texas (UTXA), which is probably *nubila*, because this species seems to be more widely distributed, especially southward, than *aldrichi* or *nubilifera*.

Biology The flight period of this relatively common species extends from mid-May to mid-October, with collection records indicating that it is more common in late summer and early fall. Adults have been recorded from peach *(Prunus persica)*, on tree trunk, on hickory *(Carya)*, and along a river. Several specimens examined were collected from Malaise traps.

At the beginning of December, 1932, R. B. Swain collected some artichoke *(Cynara scolymus)* trash at Blackjack, Missouri. Evidently larvae were feeding on the decaying leaves, etc., and in mid-March adults began to emerge.

In mid-July, 1972, rearings were initiated by using adults collected in a lowland woods along a stream near Jennings, Kansas. The field-collected males lived 33-43 days; females, 40-51 days. There was no apparent diapause, although some eclosion took longer than 1 week. Larvae fed on decaying lettuce and decaying tree leaves, but development varied. By the end of September the rearing dishes contained all 3 instars. Adults began emerging at the end of October and through mid-November. Two adults emerged in December and finally 1 in mid-January. Laboratory reared males (2) lived 81-130 days; females (5), 43-141 days. The preoviposition period for 2 females was 17 and 30 days. A pair was observed for a few minutes mating in the late morning. Their behavior was very similar to that described in other species of *Homoneura*. The prepupal period was approximately 48 hours. The pupal period for reared males was 11-12 days; females, 14-15 days.

At the end of May and the beginning of June, 1973, some 3rd-instar larvae were collected from leaf litter and plant debris at Bay's Branch Area, Iowa. A few cottonwood *(Populus deltoides)*, mulberry (*Morus* sp.), and boxelder *(Acer negundo)* were present in this low area at the edge of a reservoir. Adults emerged at the beginning and end of June.

Near the end of March, 1975, several 3rd instars were collected from leaf litter at Red Haw State Park, Iowa. One male *nubila* emerged in mid-May along with a few males of *nubilifera* and several females.

Because no distinct diapause was observed, this species is probably univoltine in the northern latitudes and bivoltine in the southern part of its range, with quiescent larvae during dry and cold periods.

Homoneura (Homoneura) nubilifera (Malloch)
(Fig. 102)

Sapromyza nubilifera Malloch, 1920: 126 [descr. - IL].
Malloch & McAtee, 1924: 21 [key], 23 [coll. rec. - MD]; Pl. 2, Fig. 23 [genitalia, ♂].
Shewell, 1965: 699 [cat., distr., - IL, IN, TN, MD].

Diagnosis Males of *nubilifera* are separable from *aldrichi* and *nubila* by having a fringe of long, fine, av TS3 bristles and S5 with an apical fringe of black setulae.

Discussion The male genitalia of *nubilifera* are similar to *aldrichi*, but differ by having the surstylus broader and the terminal processes foot-shaped, rather than fan-shaped (Figs. 102, 103). The cercus of *nubilifera* has long, dense setae at the apex, while that of *aldrichi* has long, dark, evenly-spaced setae at the apical margin.

Types Holotype: ♂, Monticello, Illinois, VI-21-1914, C. A. Hart & J. R. Malloch, along Sangamon River (INHS). Allotype: ♀, same data as holotype, VI-28-1914 (INHS). Paratypes: 1♂, same data as holotype (INHS); 2♂, Mahomet, Illinois, VII-6-1914, C. A. Hart & J. R. Malloch, along Sangamon River (INHS); 2♂, 2♀, Urbana, Illinois, VI-17-1916, C. A. Hart & J. R. Malloch, forestry (INHS); 2♂, Urbana, Illinois, VI-20-1915, C. A. Hart & J. R. Malloch (CNC, INHS); 1♀, Urbana, Illinois, VI-23-1916, C. A. Hart & J. R. Malloch (INHS).

Specimens examined 43 (31♂, 12♀) from 18 central and eastern USA localities:

IA—5♂, 3♀, 6 localities (IASU); 3♂, 3♀, Stone St. Pk., Sioux City, reared 1971, R. M. Miller; 3♂, Red Haw St. Pk., 1 mi e. Chariton, reared 1975, R. M. Miller (RMM).

IL—3♂, 3 localities (INHS, USNM, UTXA); types.

IN—5♂, Lafayette, VII-13,-23, J. M. Aldrich (CNC, USNM).

KY—1♂, Lexington, VIII-6-1920, H. Garman (UKY).

MD—1♂, Plummers Is., VI-8-1914, Schwarz & Shannon, at light, (USNM).

MO—1♂, Atherton, VIII-20-1922, C. F. Adams (PU).

TN—1♂, Hamilton Co., VI-30-1939, from peach (USNM).

Biology The flight period for this uncommon species extends from early June to mid-September, with most specimens having been collected in July and August. Adults have been recorded from peach *(Prunus persicus)*, forests, and along a river. One specimen examined was collected from a Malaise trap and another at light.

At the beginning of August, 1971, a rearing was initiated by using adults collected in a mesophytic woods at Stone State Park, Sioux City, Iowa. By early September most larvae had hatched, and 3rd instars were observed by the end of the month. Larvae fed on decaying tree leaves and lettuce in the laboratory. Adults emerged from mid-October to the end of the month. The prepupal period was approximately 48 hours. The pupal period for reared males (5) was 11-14 days; females (3), 11-12 days.

In mid-April, 1974, and toward the end of March, 1975, 3rd instars were collected in leaf litter at Red Haw State Park, Iowa, along with some larvae of *nubila*. Three males and 7 females emerged, beginning in mid-April. The prepupal period was approximately 48 hours and 1 male emerged in 10 days.

From the relatively fast development in the laboratory rearings, it is probable that at least some members start a 2nd generation in the fall. Quiescent larvae are the overwintering stage.

Homoneura (Homoneura) aldrichi NEW SPECIES
(Figs. 58, 71, 103)

Malloch & McAtee, 1924: 23 [coll. rec. - MD, 1 as *nubilifera*, MISIDENT.].

Diagnosis Males of *aldrichi* are separable from *nubila* and *nubilifera* by lacking differentiated setae on the apex of S5 and lacking long, fine, av bristles on L3 basitarsi.

Discussion The male genitalia of *aldrichi* are similar to *nubilifera*, but differ by having the surstylus narrower and the terminal processes fan-shaped, rather than foot-shaped (Figs. 102, 103). The cercus of *aldrichi* has long, dark, evenly-spaced setae at the apical margins, whereas *nubilifera* has long, dark, dense setae at the apices.

Description Total length 4-4.5 mm; wing length 3.5-4 mm. Yellow, with whitish pollinosity. Similar to *nubila* and *nubilifera*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor, aor set closer to antennal bases than por. Eye ¼th higher than wide. Face flat; parafacials about ⅓rd width of face at middle. Gena about 1/6th height of eye. Arista plumose. Head chaetotaxy: aor shorter than por, approximately ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong and well in front of suture; acr inner 2 rows, strong, outer 2 rows, setae usually complete. Legs pale yellow with av F1 ctenidium of 10-16 widely spaced setulae; F3 with a strong preapical av and ad bristle; T3 of males with fringe of long, fine, av bristles on apical half. Wings yellow with r-m and m broadly and distinctly infuscated, brown.

Male: surstylus narrow and rounded apically, apex posteriorly-directed; gonopods long and linear; terminal processes fan-shaped posteriorly with marginal setae; cercus with long, dark, evenly-spaced setae at the apical margin. Female: cercus yellow, with long, dark setae.

Types Holotype: ♂, Lafayette, Indiana, VII-11, J. M. Aldrich (USNM 75372). Paratypes: 2♂, same data as holotype (USNM); 2♂, same data as holotype except VII-23 (USNM); 1♀, same data as holotype except, VII-12 (USNM); 5♂, 5♀, Pilot Mound State Forest, Boone County, Iowa, VI-23-1972, R. M. Miller (CNC, USNM).

Remarks This species is named in honor of its collector, John M. Aldrich, and his contribution to the study of the Diptera. It must be noted that female paratypes may prove to be different species, because Aldrich also collected *nubilifera* at Lafayette and I collected *nubila* at Pilot Mound State Forest.

Specimens examined 19 (13♂, 6♀) from 6 central and eastern USA localities:

AR—1♂, Fayetteville, VIII-10-1907 (UAR).

IA—1♂, Ledges St. Pk., Boone Co., VII-28-1972, W. B. Stoltzfus (IASU); 5♂, 5♀, paratypes (CNC, USNM).

IN—1♂, holotype; 4♂, 1♀, paratypes.

MD—1♂, Cabin John Bridge, VI-14-1913, R. C. Shannon (USNM).

Biology The flight period for this rare species, from the collection records, begins in mid-June and ends mid-August, but probably extends through September.

In late June, a rearing was attempted by using adults collected from a very small ravine covered with cottonwood *(Populus deltoides)* and black raspberry (*Rubus* sp.) at Pilot Mound State Forest, Iowa. The larvae fed on decaying lettuce and tree leaves, and 2 puparia were formed in October and November but no adults emerged. This species is probably univoltine.

Homoneura littoralis incertae sedis

Homoneura (Homoneura) littoralis (Malloch)
(Figs. 83, 105, 106)

Sapromyza littoralis Malloch, 1915: 47 [descr. - MI].

Malloch & McAtee, 1924: 22 [key].

Johnson, 1925a: 256 [coll. rec. - VT].

Criddle, 1926: 104 [coll. rec. - QUE, ONT, MAN].

Petch & Maltais, 1932: 65 [coll. rec. - QUE].

Shewell, 1938: 135 [key], 140 [coll. rec. - QUE, ONT, MAN]; 136 (Pl. 13) Fig. 45 [genitalia, ♂].

Osborn & Knull, 1939: 256 [coll. rec. - OH].

Chagnon, 1952: 29 [coll. rec. - QUE].

Shewell, 1965: 698 [cat., distr. - n. ALTA to PEI, s. to NY].

Cole, 1969: 373 [distr. - ALTA].

Diagnosis This large, clear-winged species is characterized by having arista short pubescent, a swollen frons with the parafacials ⅔rds the width of the middle of the face, and small eyes with the gena ½ their height. Males are unique in having setulae on the venter of the L3 trochanter and basal surface of the F3 (Fig. 83); females are unique in having some dorsal setulae on the cercus (Fig. 106).

Discussion This species is most similar to the *harti* group, but can be separated by having 2 apical T2 spurs, whereas species in the *harti* group usually have 3-4. Males of *harti* group lack setulae on the T3 trochanter and F3 and have pointed aedeagus, whereas the aedeagus is rounded apically with a small, anteriorly-directed point in *littoralis* (Fig. 105).

Types Lectotype: ♂, South Haven, Michigan, VII-14-1914, C. A. Hart, sweeping on the lake shore (INHS). Allolectotype: ♀, same data as lectotype (INHS). Paralectotypes: 1♂, 1♀, same data as lectotype (INHS).

Specimens examined 374 (191♂, 183♀) from 66 north central and northeastern NA localities:

ALTA—1♂, McMurray, VI-6-1953, G. E. Ball (CNC).

CO—1♂, Reggen, VI-16-1936, R. Swain (COSU); 1♂, Keenesburg, VI-11-1961, W. R. M. Mason, sandhills (CNC).

IA—1♂, Ames, V-26-1952, M. L. Fairchild (IASU); 1♀, Lime Springs, VI-24-1972, R. R. Pinger, Jr. (IASU).

IL—10♂, 15♀, 4 localities (INHS, USNM).

MA—5♂, 13♀, 2 localities (FSCA, USNM, UTXA).

MAN—13♂, 16♀, 7 localities (CNC, USNM).

MI—13♂, 30♀, 15 localities (SEM, UMI, UNMI); types.

MN—2♂, 1♀, 3 localities (IASU, UMN, USNM).

ND—1♂, McLeod, VI-20-1939, D. G. Denning (UMN); 1♂, Leonard, V-24-1939, D. G. Denning (UMN).

NE—6♂, 5♀, Valentine, V-8-1950, Hicks, Slater, & Laffoon (IASU).

NJ—2♀, Seaside Park, VII-1915, VI-1916, C. W. Johnson (MCZ).

NS—53♂, 13♀, Sable Is., VII-1-13-1967, D. M. Wood (CNC).

NY—2♂, 7♀, Cold Springs Harbor, Long Is., VI-25, VII-9,13-1931, C. H. Curran (AMNH, CNC).

OH—1♂, Sandusky, Cedar Point, VI-8-1902, J. S. Hine (OHSU).
ONT—30♂, 27♀, 10 localities (CAS, CNC, OHSU, UCALA, USNM, UTXA).
PA—1♂, 2♀, 2 localities (FEM, PADA).
QUE—41♂, 42♀, 5 localities (AMNH, UCALA, UM, UTXA).
SASK—1♂, 1♀, Hatton, VI-11-1929, K. M. King, R. Glen (CNC); 1♀, Great Sand Hills, w. Swift, V-27-1939, A. R. Brooks (CNC).
SD—5♂, 3♀, Lake Campbell, VI-20-1935, A. B. Peterson & D. E. Herreman (SDSU).
WI—1♀, Devils Lake, VII-7-1933, A. L. Melander (USNM); 1♀, University of Wisconsin Campus, Madison, VII-15-1915, A. C. Burrill (UWI).

Remarks Johnson (1925a) reported this species from Vermont, and Shewell (1965) included the Prince Edward Island, from which I have not seen specimens.

Biology The flight period for this abundant species begins early in May and extends through mid-September. Collections are most successful in June and July. Specimens have been collected *in copula* June 29 (Manitoba), July 6 (Massachusetts), and August 9 (Michigan); Shewell (1938) reported pairs *in copula* on July 14 and 15 (Quebec). Adults have been collected from *Elaeagnus commutata* (silverberry), sand dunes, and quite commonly along lake shores.

Homoneura harti Group

Diagnosis This group of 3, medium-sized to large, clear-winged species is characterized by the following combination of characters: (1) swollen frons, with gena ½-⅓rd height of eye; (2) parafacials approximately ⅔rds width of middle of face; (3) 1+3 dc, presutural dc strong, well-removed anteriorly from the suture; (4) arista long pubescent; (5) preapical av and ad F3 bristles present; (6) usually 3-4 distinct apical T2 spurs present.

Discussion The wings of this group are large and immaculate (Figs. 65, 66). The males are characterized by having the anterior L2 claws enlarged and slightly recurved (Figs. 81, 82), and genitalia are very similar, with specific differences in the pl S5 processes. The females have the T7 about twice as large as T6 and cylindrical, very small cercus (Fig. 136).

Key to Species of *harti* Group

1. Setae of head, 2nd antennal segment, hypopygium and cercus yellow or light brown 2
   Setae the usual dark brown or black .... *psammophila*, p. 203
2. Gena ½ height of eye .... *harti*, p. 201
   Gena ⅓rd height of eye .... *ocula*, p. 202

Homoneura (Homoneura) harti (Malloch)
(Figs. 135, 136)

Sapromyza harti Malloch, 1914: 32 [descr. - IL]; Pl. II, Fig. 3 [head], Fig. 7 [abdomen, ♀], Fig. 8 [abdomen, ♂], Fig. 14 [F3, ♂].
Malloch & McAtee, 1924: 21, 22 [key].
Criddle, 1928: 100 [coll. rec. - ONT].
Shewell, 1965: 698 [cat., distr. - s. ALTA to s. ONT, IL, WY, KS, OK].
Cole, 1969: 373 [distr. - ALTA, WY].

Diagnosis This large, clear-winged species can be distinguished from the closely related *ocula* in that the gena is ½ the height of the eye, rather than ⅓rd, and from *psammophila* by the light brown, rather than black, 2nd antennal setae.

Discussion Male genitalia are similar except for the broad and expanded pl S5 processes in *ocula*, foot-shaped in *psammophila*, and narrowed in *harti* (Figs. 133-135). The cercus of females with pale setae only.

Types Lectotype: ♂, Quincy, Illinois, VIII-12-1889, C. A. Hart, swept from sand bar [Hart Acc. No. 553] (INHS). Allolectotype: ♀, same data as lectotype (INHS). Paralectotypes: 1♂, same data as lectotype (INHS); 2♀, Quincy, Illinois, VIII-7-1889, C. A. Hart, sweeping willow & *Xanthium* [Hart Acc. No. 544] (INHS).

Specimens examined 342 (142♂, 200♀) from 82 central NA localities:
ALTA—2♂, 3♀, 3 localities (CNC, UALTA).
AR—5♂, 3♀, 2 localities (UAR).
CO—7♂, 16♀, 5 localities (CNC, COSU, IASU); 3♂, 7♀, 6 mi e. Castle Rock, reared 1972, R. M. Miller (RMM).

IA—8♂, 5♀, 5 localities (IASU).
IL—30♂, 34♀, 7 localities (CAS, IASU, INHS); types.
IN—1♀, Gibson Co., VI-6-1958 (PU).
KS—7♂, 13♀, 11 localities (MCZ, OHSU, SEM, USNM).
MAN—2♂, 3♀, 2 localities (CNC, USNM, UTXA).
MI—1♂, 5♀, 5 localities (IASU, UMI).
MN—1♀, Isanti Co., VI-13-1938, D. G. Denning (UMN).
MT—1♀, Powderville, VI-15-1916, R. Kellogg (USNM).
NE—3♂, 9♀, 7 localities (CNC, IASU, MCZ, OHSU, UNE, USNM, UTXA).
NM—35♂, 38♀, White Sands Natl. Monument, Otero Co., VI-20-1947, C. P. Stroud, near picnic area, sweeping poplars (WASU).
OH—2♀, Lucas Co., VI-24-1934, M. Auten (OHSU).
OK—11♂, 15♀, 5 localities (OKSU).
ONT—5♂, 9♀, 5 localities (AMNH, CAS, CNC).
SD—14♂, 20♀, 7 localities (IASU, SDSU).
TX—2♂, 1♀, 2 localities (USNM).
WI—2♂, 5♀, 2 localities (UWI).
WY—3♂, 6♀, 6 localities (AMNH, IASU, UWY).

Biology The flight period for this abundant species begins in mid-May and extends to mid-October, with specimens most commonly collected during the months of June, July, and August. Several adults have been collected from willow *(Salix)*, locust *(Robinia)*, and cotton *(Gossypium herbaceum)*; and 1 female each from wheat *(Triticum aestivum)* and melon *(Cucurbita)*. Many adults have been collected from sand dunes and also in association with *Elaeaganus commutata* (silverberry) and *Betula occidentalis* [= *frontinalis*] (water birch). Numerous specimens have been collected from poplars (*Populus* sp.).

In early July, 1972, rearings were initiated by using adults collected from tall grass in a lowland pasture near Castle Rock, Colorado. Eggs were laid singly on decaying lettuce and leaves. Eclosion and larval stadia, especially the 3rd instar, were highly variable. Larvae showed strong negative phototactic responses and burrowed immediately when uncovered. They seemed to prefer feeding on freshly decaying lettuce and even the Brewer's yeast-honey mixture provided as food for adults. Adults began emerging in the laboratory on November 1. Mating was observed only once, briefly. The male was situated dorsally and faced in the same direction as the female, with his head near the midpoint of the female's thorax. His foretarsal claws were hooked on the suture ridge between the notopleuron and mesopleuron, just anterior to the posterior np of the female. The recurved, anterior, mid-tarsal claws were hooked to the bases of the female's wings and the hindtarsi were appressed on the half-outstretched wings.

Preoviposition period for 3 reared females ranged from 32-45 days. The total larval period for 1 specimen was approximately 85 days; prepupal period lasted 48 hours; and pupal period for 10 reared adults ranged from 14-16 days. Adults lived up to 142 days in the laboratory. The time required to complete a life cycle for 1 rearing was 130 days.

Laboratory rearings indicated that this species is probably at least partially bivoltine, especially in the southern part of its range. No diapause was evident in the rearings.

Homoneura (Homoneura) ocula NEW SPECIES
(Figs. 65, 74, 81, 133)

Diagnosis This large, clear-winged species can be distinguished from the closely related *harti* and *psammophila* by the gena being ⅓rd the height of the eye, rather than ½.

Discussion Male genitalia are similar except for the narrowed pl S5 processes in *harti*, foot-shaped in *psammophila*, and broad and expanded in *ocula* (Figs. 133-135). *H. ocula* is most similar to *harti* in size, possessing 3-4 distinct apical T2 spurs and pale yellow to light brown head setae.

Description Total length 4-4.5 mm; wing length 4-4.5 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *harti* and *psammophila*.

Frons swollen in profile; por equidistant between iv and aor, set in narrow shining plates. Parafacials about ⅔rds width of face at middle. Gena approximately ⅓rd height of eye. Head setae pale yellow to light brown; arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc subequal to iv; por subequal to ov; pvt shorter than aor.

Thorax brownish-yellow, subshining, covered with whitish pollinosity. Chaetotaxy: 1 + 3 dc, presutural dc strong, well-removed anteriorly from suture; acr with 2 inner rows weak bristles, 2 incomplete outer rows setae. Legs yellow with av F1 ctenidium of 8-11 closely spaced, weak setulae; F3 with 1-4 preapical av, 1 ad and 0 pv bristles. T2 with 3-4 apical spurs, a and pv approximately ⅓rd and ⅔rds of av, respectively. Wings yellowish, immaculate.

Male: p1 S5 processes broad, expanded lobe; T6 about 1.5 times longer than T5; surstylus arm-shaped, narrowed posteriorly, crenulated apically; aedeagus pointed apically; cercus short; light yellow to pale brown setae on epandrium and cercus. Female: T7 cylindrical, about 1.5 times longer than T6; cercus very small, yellow, with light brown setae.

Types Holotype: ♂, Fredonia, Arizona, VI-16-1951, G. F. Knowlton [genitalia preserved in glycerin in microvial] (USNM 75373). Allotype: ♀, same data as male (USNM). Paratypes: 1♂, 2♀, Indian Creek, San Juan Co., Utah, VII-27-1938, G. F. Knowlton & F. C. Harmston (CNC, UTSU); 1♂, Moab, Utah, VI-25-1938, G. F. Knowlton & F. C. Harmston (RMM); 1♀, Fort Duchesne, Utah, VII-21-1953, G. F. Knowlton (USNM); 1♀, Syracuse, Utah, VI-7-1933, G. F. Knowlton (UTSU); 1♀, 10 mi se. Vernon, Wasatch National Forest, Utah, VII-8-1972, R. M. Miller (RMM); 1♀, 2 mi se. DeBeque, Colorado, VII-9-1972, W. B. Stoltzfus (IASU); 1♀, Zion Canyon, Utah, VI-17-1919 (UTSU); 1♀, Kane Co., Kanab Riv., VI-16-1961, W. J. Hanson (UTSU).

Biology The flight period for this rare, central western species begins in early June and extends through late July. Its range overlaps with that of *psammophila*, but it is evidently not associated with sand dune habitats as is *psammophila*. *H. ocula* probably occurs in grass-shrub habitats near water as does *harti* in central and eastern North America.

Homoneura (Homoneura) psammophila NEW SPECIES
(Figs. 66, 75, 82, 134)

Diagnosis This medium-sized, clear-winged species can be distinguished generally by its smaller size, 2nd antennal setae being black (Fig. 75), rather than light brown, and males possessing a row of weak premarginal bristles on the lateral aspects of T6, which is not as developed in *harti* or *ocula*.

Discussion *H. psammophila* has the usual black setal coloration, whereas *harti* and *ocula* have yellow to light brown setae, especially on the head and cerci, with only the bristles distinctly black. Male genitalia are similar except for the p1 S5 process being a simple, narrowed lobe in *harti*, a broad, expanded lobe in *ocula*, and a somewhat foot-shaped structure in *psammophila* (Figs. 133-135).

Description Total length 3.25-4.25 mm; wing length 3.5-4 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *harti* and *ocula*.

Frons swollen in profile; por equidistant between iv and aor. Face slightly concave; parafacials about ⅔rds width of face at middle. Gena approximately ½ height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc subequal to iv; por subequal to ov; pvt shorter than aor.

Thorax brownish-yellow, subshining, covered with sparse whitish pollinosity. Chaetotaxy: 1+3 dc, presutural dc strong, well-removed anteriorly from suture; acr with 2 inner rows of weak bristles, 2 incomplete outer rows setae. Legs yellow with av F1 ctenidium of 8-11 closely spaced, weak setulae; F3 with 1-4 preapical av, 1 ad and 0 pv bristles. T2 usually with only 2 distinct apical spurs. Wings yellowish, immaculate.

Male: p1 S5 processes foot-shaped, small toe directed anteriorly; T6 about 1.5 times longer than T5; a row of weak premarginal bristles about ½ length of marginal row on lateral aspect of T6; surstylus arm-shaped, narrowed posteriorly, crenulated apically; aedeagus pointed apically; cercus short, with short, light, apical setae. Female: T7 cylindrical, about 1.5 times longer than T6; cercus very small, yellow, with brown setae.

Types Holotype: ♂, 8 mi (12.8 km) southwest of Jericho, Juab Co., Utah, VII-9-1971, C. A. Toft, on *Psoralea lanceolata*, in shifting-dunes habitat (USNM 75374). Allotype: ♀, same data as holotype (USNM). Paratypes: 15♂, 7♀, same data as holotype (CAS, CNC, IASU, INHS, USNM); 7♂, 2♀, St. Anthony, Idaho, VI-23-1961, W. F. Barr, sand dunes, sweeping *Psoralea lanceolata* (UID, USNM).

Specimens examined 74 (44♂, 30♀) from 13 central western USA localities:

CO—1♂, Great Sand Dunes, Alamosa Co., VII-20-21-1954, H. E. & M. A. Evans (COU).

ID—5♂, 11♀, 3 localities (UID); 7♂, 2♀, paratypes (UID, USNM).

UT—13♂, 8♀, 5 localities (IASU, KSU, UTSU); holotype; allotype; 15♂, 7♀ paratypes.

WY—1♂, Powder River, VIII-1-1950, R. R. Dreisbach & R. K. Schwab (USNM); 1♂, 1♀, nr. Douglas, VII-22-1973, W. B. Stoltzfus (IASU).

Biology The flight period for this rather uncommon species begins in early June and extends to early August. Most of the collection records indicate that this species is associated with sand dune habitats and *Psoralea lanceolata* (a type of bread-root or Indian turnip).

In the summer of 1971 a long series of specimens collected on *Psoralea lanceolata* in shifting sand dunes habitat near Jericho, Utah, was received from Cathie A. Toft. According to her observations (pers. com.) the flies infested only the plants infected with an orange rust (*Uromyces psoraleae* var. *typica* Arth.). This rust is specific to *P. lanceolata* in the Great Basin west of Colorado. When the flies were present, they were found in large numbers. She never found the flies on any *Psoralea* except in Juab Co., but did find the rust-infected plants in other localities.

I suspect that this species has only 1 generation per year. It probably occurs only at specific times when rust is present on *Psoralea* and might serve as a food source for the adults.

Homoneura bakeri incertae sedis

Homoneura (Homoneura) bakeri NEW SPECIES
(Figs. 59, 108)

Diagnosis This small species is closely related to *setitibia* by having 2-4 strong, preapical av F3 bristles. However, it is easily distinguished by having the av F1 ctenidium of 3-5 very weak setulae, similar to that found in *citreifrons* (Fig. 5), and the r-m and m lightly bordered.

Discussion T7 of males is distinctly humped dorsally, as in *inaequalis* (Figs. 107, 108). Male genitalia of *bakeri* are very similar to *trochantera* (Fig. 109), but the long, linear cercus and pointed aedeagus easily distinguish *bakeri*. Male genitalia of *bakeri* are also similar to *knowltoni*, (Fig. 115), but the pl S5 processes have minute apical setulae in *knowltoni*, whereas *bakeri* has small serrations apically. Females of *bakeri* are identifiable by the heavily setose S8 and S9 and moderately long and apically darkened cercus.

Description Total length 3-3.25 mm; wing length 3.2-3.4 mm. Brownish-yellow, with sparse whitish pollinosity. Similar to *knowltoni* and *trochantera*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face slightly concave; parafacials about ½ width of face at middle. Gena about ¼ height of eye. Arista long pubescent. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong, well-removed anteriorly from the suture; acr with 2 inner rows of weak bristles, 2 incomplete outer rows of setae.

Legs yellow, with av F1 ctenidium of 3-5 widely spaced, very weak setulae; F3 with 2-4 strong av, with ad and without pv bristles. Wings yellowish with slightly darkened crossveins.

Male: pl S5 processes somewhat fan-shaped, weakly serrated marginally; T6 about twice as long as T5; surstylus foot-shaped, with toe directed posteriorly; aedeagus long, tubular, pointed apically; cercus very long, narrowed posteriorly, with apical setae slightly longer than others and brown. Female: T7 cylindrical, slightly longer than T6; S8 and S9 heavily setose; cercus moderately long, dark apically, with dense brown setae.

Types Holotype: ♂, Laguna Beach, Southern California, C. F. Baker [genitalia preserved in glycerin in microvial] (USNM 75375). Allotype: ♀, Pasadena, California, J. M. Aldrich (USNM). Paratype: 1♀, Big Sur, Monterey Co., California, VIII-23-1951, W. H. Lange (UCAD).

Remarks This species is named after its collector, Charles F. Baker, for his early contribution to California Diptera.

Biology Evidently nothing is known about the biology of this very rarely collected, Californian species. The allotype was misidentified as *Sapromyza innuba* Giglio-Tos and reported by Melander (1913:67).

Homoneura inaequalis incertae sedis

Homoneura (Homoneura) inaequalis (Malloch)
(Figs. 73, 107)

Sapromyza inaequalis Malloch, 1914: 32 [key], 35-36 [descr. - IL]; Pl. II, Fig. 16 [head, ♀].
Malloch & McAtee, 1924: 21 [key].
Shewell, 1965: 698 [cat., distr. - s. BC, ALTA and SASK].
Cole, 1969: 373 [distr. - BC, ALTA, SASK].

Diagnosis This small species can be recognized by having the r-m and m lightly bordered, the arista short pubescent (Fig. 73), L3 trochanter possessing setulae ventrally and lacking a strong preapical av F3 bristle.

Discussion This species is similar to *setula*, but can be distinguished by the plumose arista of *setula*. Males also have a dorsal T7 hump, as found in *bakeri*, and possess unique, small, p1 S5 processes that bear 6-8 strong setulae (Fig. 107).

Types Holotype: ♂, Urbana, Illinois, V-9-1911, C. A. Hart [Acc. No. 16287] (INHS). Allotype: ♀, Urbana, Illinois, V-28-1911, C. A. Hart [Acc. No. 15693] (INHS).

Specimens examined 39 (17♂, 22♀) from 20 north-central NA localities:

ALTA—4♂, 6♀, 6 localities (BMNH, CNC).

BC—2♀, Vernon, VI-9-1937, H. Leech, on leaves of *Crataegus* (CNC).

IA—1♀, Stone St. Pk., Sioux City, VI-17-1957, J. L. Laffoon (IASU); 1♂, 1♀, Bay's Branch Area, Guthrie Co., VI-8-1972, R. M. Miller (RMM).

IL—types.

KS—1♂, Riley Co., V-6 (SEM).

MI—1♂, 1♀, Midland Co., V-30-1935, G. Steyskal (USNM).

SASK—9♂, 9♀, 6 localities (CNC).

SD—1♂, Winner, VII-3-1924 (SDSU).

Remarks I have also examined 1 female from Arizona [SW Research Station, 8 km sw. Portal, V-23-VI-5-1965, C. W. Sabrosky, 1,646 m, Malaise trap (USNM)], which is very similar to *inaequalis*, but has slightly larger eyes. Since it is far outside the known range of *inaequalis*, there is a good possibility that it is a new species. A male from this area would help decide the status of this specimen.

Biology The flight period for this uncommon species begins in early May and extends through late July, with most collection records in June. Two females have been collected on leaves of *Crataegus* (red haw or hawthorn).

Homoneura setula incertae sedis

Homoneura (Homoneura) setula NEW SPECIES
(Figs. 55, 77, 84, 111)

Melander, 1913: 74 [coll. rec. - OR, as var. *nubila*, MISIDENT.].
Cole & Lovett, 1921: 323 [list - OR, same as Melander, 1913].

Diagnosis This medium-sized species has both r-m and m narrowly bordered with brown (Fig. 55). It can be recognized by having the arista plumose (Fig. 77), L3 trochanter possessing setulae ventrally, and lacking strong preapical av F3 bristles (Fig. 84).

Discussion This species is similar to *inaequalis* in having L3 trochanter with setulae, but *inaequalis* has arista short pubescent. Males of *setula* have large, fan-shaped, strongly crenulated, p1 S5 processes and small gonopods (Fig. 111). Superficially the genitalia are similar to those found in the *trochantera* group (Figs. 109, 110).

Description Total length 3-3.5 mm; wing length 3-3.5 mm. Brownish-yellow, with very sparse whitish pollinosity. Similar to *inaequalis* and *trochantera*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face flat; parafacials about ½ width of face at middle. Gena about ¼th height of eye. Arista plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong, well-removed anteriorly from suture; acr with 2 inner rows weak bristles; 2 incomplete outer rows setae. Legs yellow, with L3 trochanter with black setulae ventrally; av F1 ctenidium of 6-9 closely spaced setulae; F3 with preapical ad, weak row of av and without pv bristles. Wing yellowish with both r-m and m narrowly bordered brown.

Male: p1 S5 processes fan-shaped, strongly crenulated marginally; T6 about twice length of T5; surstylus arm-shaped, narrowed posteriorly, minutely crenulated apically; gonopods small, linear; aedeagus rounded apically; cercus long, narrowed posteriorly, with apical setae longer than other setae. Female: T7 cylindrical, longer than T6; cercus dark.

Types Holotype: ♂, Colton, California, VII-5-1951, J. C. Hall (CAS 13035). Allotype: ♀, same data as holotype (CAS). Paratypes: 5♂, 1♀, same data as holotype (UCAD); 3♂, 1♀, Big Tujunga Cn., Los Angeles Co., California, VII-19-1952, R. X. Schick (UCALA); 2♂, 1♀, American River, Sacramento, California, VI-15-1966, M. S. Wasbauer (CADA); 1♂, 1♀, Almota, Washington, VI-24-1911, A. L. Melander (USNM); 1♂, 1♀, Mt. Diablo, Washington, VII-1937, M. A. Cazier (AMNH).

Specimens examined 29 (17♂, 12♀) from 14 western USA localities:
CA—4♂, 3♀, 6 localities (CADA, CAS, CNC, UCAB, USNM, UTXA); holotype, allotype; 10♂, 3♀, paratypes.
OR—1♀, Hood River, J. M. Aldrich (USNM).
WA—2♀, 2 localities (USNM, WASU); 2♂, 2♀, paratypes.

Biology This uncommon species has a flight period beginning the end of May and extending through mid-September, with most collection records in June and July. One specimen has been collected at 914 m. Several adults have been collected along rivers.

Homoneura trochantera Group

This is a tentative grouping of 2, medium-sized California species, which are very closely related.

Diagnosis This group can be distinguished by the following combinations of characters: (1) L3 trochanter with black setae ventrally (Fig. 86); (2) av F1 ctenidium of 6-8 weak, widely spaced setulae (Fig. 79); (3) preapical av F3 bristles absent and ad bristles weak; (4) preapical d T3 bristle about ⅔rds width of T3 at its insertion.

Discussion Male genitalia are very similar to those of *setula*, but *setula* possesses small gonopods, which are not present in the *trochantera* group. The small preapical d T3 bristles are similar to those in the *occidentalis* group.

Key to Species of *trochantera* Group

1. Wing maculated (Fig. 48) . . . . *trochantera*, p.206
[see couplet 7, p. 178]
Wing with only r-m and m bordered (Fig. 57) . . . . *californica*, p.207

Homoneura (Homoneura) trochantera NEW SPECIES
(Figs. 48, 79, 86, 109)

McDonald, Heed & Miranda, 1974: 79 [larval ecology - CA: as *Homoneura* n. sp.].

Diagnosis This medium-sized species is characterized by having both r-m and m broadly bordered with brown; apical R_{2+3}, preapical and apical R_{4+5}, and apical M_{1+2} spots with brown. It can also be distinguished from *californica* by having short plumose arista rather than plumose.

Discussion Male genitalia of *trochantera* and *californica* are very similar, although the p1 S5 processes are more fan-shaped and have stronger crenulations in *trochantera* (Figs. 109, 110).

Description Total length 3-3.5 mm; wing length 3-3.4 mm. Brownish-yellow, with very sparse whitish pollinosity. Similar to *californica*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face nearly flat; parafacials about ½ width of face at middle. Gena about 1/5th height of eye. Arista short plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por, aor = ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong; acr with 2 inner rows weak bristles, 2 outer rows setae.

Legs yellow, L3 trochanter with 3-5 black setae ventrally; av F1 ctenidium of 6-10 widely spaced, weak setulae; F3 usually with weak preapical ad and av bristles; T3 with preapical d bristle about ⅔rd width of T3 at its insertion. Wing yellowish with r-m and m bordered brown; apical R_{2+3}, preapical and apical R_{4+5}, and apical M_{1+2} spots brown, usually with apical R_{2+3} spot large and distinct and others, especially M_{1+2}, may be weak.

Male: p1 S5 processes broad, somewhat fan-shaped, strongly crenulated anteriorly, sharply pointed posteriorly; T6 slightly longer than T5 and with slightly stronger marginal bristles; surstylus arm-shaped, narrowed posteriorly, serrated apically; aedeagus slightly pointed apically; cercus long, narrowed posteriorly, with apical setae longer than other setae. Female: T7 cylindrical, longer than T6; S8 and S9 heavily setose; cercus black.

Types Holotype: ♂, Big Dalton Dam, Los Angeles County, California, VII-13-1950, W. C. Bentinck (CAS 12999). Allotype: ♀, same data as holotype (CAS). Paratypes: 1♂, 3♀, same data as holotype (UCAB); 3♂, 3♀, Snow Crest Camp, San Bernadino County, California, IX-12-1953, E. I. Schlinger (UCAD); 5♂, 1♀, Muir Woods, Marin County, VIII-30-1908, J. C. Bradley (CNC, CU); 11♂, Big Sur, California, X-5-1946, A. L. Melander (USNM).

Specimens examined 84 (52♂, 32♀) from 29 far western USA localities:

CA—29♂, 24♀, 23 localities (CAS, CNC, CU, LACM, UCAB, UCAD, UCALA, USNM, UTXA); types; 1♂, 5 mi w. Lake Berryessa, Napa Co., reared 1973, J. F. McDonald (RMM).

OR—1♂, Kerby, IX-18-1934, A. L. Melander (USNM).

Biology The flight period for this relatively common species begins in late April and extends through mid-October. Several adults have been collected from *Aralia californica* (spikenard) and from Malaise traps.

McDonald, Heed, & Miranda (1974) reared this species from larvae found in fermenting leaves of the California bay *(Umbellularia californica)* that were collected in early February, 1973, from Napa County, California. In early April, McDonald sent me 1 puparium within a leaf for examination; the adult had emerged by the time it was received.

I suspect that this species has 1 generation per year, with the larvae as the overwintering stage.

Homoneura (Homoneura) californica NEW SPECIES
(Figs. 57, 110)

Diagnosis This small species is characterized by having both r-m and m bordered with brown (Fig. 57), but lacking apical spots as found in *trochantera* (Fig. 48). *H. californica* can also be identified by plumose arista, rather than short plumose as in *trochantera*.

Discussion Male genitalia of *californica* and *trochantera* are very similar, although the pl S5 processes are not as fan-shaped and with weaker crenulations in *californica* and the aedeagus of *californica* is more rounded (Figs. 109, 110).

Because the wing pattern of both species is the strongest difference, *californica* could be a variation of *trochantera*, but there are no indications along the veins where normal spots might occur.

Description Total length 2.75-3.25 mm; wing length 3-3.3 mm. Brownish-yellow, with very sparse whitish pollinosity. Similar to *trochantera*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face nearly flat; parafacials about ½ width of face at middle. Gena about 1/5th height of eye. Arista plumose. Head chaetotaxy: aor shorter than por, ½ iv; oc = por; aor = ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong; acr with 2 inner rows weak bristles, 2 outer rows setae. Legs yellow, L3 trochanter with 3-5 black setae ventrally; av F1 ctenidium of 6-10 widely spaced, weak setulae; F3 usually with weak preapical ad and av bristles; T3 with preapical d bristle about ⅔rd width of T3 at its insertion. Wings yellowish with r-m and m bordered brown.

Male: pl S5 processes linear, somewhat fan-shaped, weakly crenulated anteriorly, sharply pointed posteriorly; T6 slightly longer than T5 and with slightly stronger marginal bristles; surstylus arm-shaped, narrowed posteriorly, serrated apically; aedeagus rounded apically; cercus long, narrowed posteriorly, with apical setae longer than other setae. Female unknown.

Types Holotype: ♂, Forest Home, California, VIII-26-1944, A. L. Melander [genitalia preserved in glycerin in microvial] (USNM 75376). Paratype: ♂, Dark Canyon, California, VII-10-1949, M. R. Wheeler (USNM).

Biology Evidently nothing is known about the biology of this very rarely collected, California species.

Homoneura setitibia Group

Diagnosis This group of 4, small to medium-sized species can be distinguished by the following combination of characters: (1) a row of at least weak preapical av and 1 strong preapical ad F3 bristles; (2) preapical d T3 bristle longer than width of T3 at its insertion; (3) 1+3 dc, presutural dc strong, well-removed anteriorly from the suture; (4) 5th TS3 segment yellow.

Discussion This somewhat artificial grouping of species has basically similar male genitalia, long, linear cerci and marginal T6 bristles longer than those of T5. *H. setitibia* and *utahensis* are very closely related, having similar chaetotaxy.

Key to Species of *setitibia* Group

1. Wing with r-m and m bordered and apical spots usually weak; additional weak bristles adjacent mp . . . . . *shewelli*, p. 208 [see couplet 6, p. 178].
   Wing immaculate or at most r-m and m darkened; only setae adjacent mp 2
2. Preapical row of av F3 bristles at most weak . . . . . *knowltoni*, p. 209
   Preapical row of av F3 bristles strong 3
3. Preapical d T3 bristle 4 times longer than width of T3 at its insertion in ♂, slightly longer than T3 in ♀ . . . . . *setitibia*, p. 209
   Preapical d T3 bristle 2 times longer than width of T3 at its insertion in ♂, subequal to T3 in ♀ . . . . . *utahensis*, p. 210

Homoneura (Homoneura) shewelli NEW SPECIES
(Figs. 56, 116)

Diagnosis This medium-sized, weakly spotted species is unique by having 1-3 additional, weak bristles adjacent to and about ⅓rd the length of the mp.

Discussion The r-m and m of *shewelli* are lightly bordered, and there are slight indications of apical R_{2-3}, R_{4-5}, and M_{1-2} spots (Fig. 56) similar to those found in *wheeleri* (Fig. 52). *H. wheeleri* does not possess a presutural dc, whereas *shewelli* has a strong presutural dc.

Male genitalia have pl S5 processes that are more rounded apically and lobe-like in *shewelli* (Fig. 116), but somewhat foot-shaped in the other species of the group (Figs. 113-115). Females have distinct black cerci, which are yellow in the other species.

Description Total length 3.5-4 mm; wing length 3.75-4 mm. Brownish-yellow, with sparse, whitish pollinosity. Similar to *setitibia* and *utahensis*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face slightly concave; parafacials about ½ width of face at middle. Gena about ¼th height of eye. Arista short plumose. Chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong, well removed anteriorly from suture; acr with 2 inner rows weak bristles, 2 incomplete outer rows setae; 1 mp, with 1-3 additional, adjacent smaller bristles, ⅓rd length of mp. Legs yellow, with av F1 ctenidium of 8-11 widely spaced, weak setulae; F3 with preapical ad, without preapical av or pv bristles. Wing yellowish with r-m and m bordered with light brown; apices of R_{2-3}, R_{4-5}, and M_{1-2} clouded or at least darkened; most of the ultimate sections of M_{1-2} darkened.

Male: T6 slightly longer than T5, with marginal T6 bristles slightly longer than T5 bristles; pl S5 processes lobe-like, slightly knobbed posteriorly, with 4-5 widely spaced, minute setulae apically; surstylus long, evenly tapering, and curved posteriorly to blunt tips, which are minutely serrated apically and have a small ventrally directed spine; aedeagus long, tubular, rounded apically; cercus long, basally with dense, short, dorsal setae, apically with longer setae. Female: T7 cylindrical, slightly longer than T6; cercus black, with long, black setae.

Types Holotype: ♂, Jumping Pd. Cr., 20 mi (32 km) w. Calgary, Alberta, VIII-8-1962, K. C. Herrmann (CNC 15414). Allotype: ♀, same locality as holotype, VII-3-1962, K. C. Herrmann (CNC). Paratypes: 1♀, same data as holotype (CNC); 1♂, same locality as holotype, VII-3-1962, K. C. Herrmann (CNC); 1♀, Robson, British Columbia, VII-26-1947, H. R. Foxlee (CNC); 1♂, Vernon, British Columbia, VIII-10-1947, H. B. Leech, on cicadellid-infested *Populus trichocarpa* (CAS); 1♂, 10 mi (17 km) n. McCall, Idaho, VI-14-1962, B. A. Foote (RMM); 1♂, Wilson Creek, Nye Co., Nevada, IX-12-1963, R. C. Bechtel, elevation 2,377 m, light trap (NVSDA); 1♀, Blacksmith Fork Canyon, Cache Co., Utah, VIII-14-1965, W. J. Hanson, Malaise trap (UTSU); 1♂, 1♀, Green Canyon, Cache Co., Utah, VIII-1-3,7-1967, W. J. Hanson, Malaise trap (USNM); 1♀, Mendon Cold Springs, Cache Co., Utah, IX-3-1965, W. J. Hanson, Malaise trap (RMM); 1♀, Bear River R. S., Summit Co., Utah, VIII-5-12-1971, Knowlton & Hanson, Malaise trap (UTSU); 1♂, Heber, Utah, VII-5-1949, F. C. Harmston (CNC); 1♂, Heber, Wasatch Co., Utah, VIII-18-1966, G. R. Knowlton (UTSU); 1♀, Willard Basin, Weber Co., Utah, VIII-10-1967, K. J. Capelle, Malaise trap (UTSU).

Remarks This species is named in honor of Guy E. Shewell for his many contributions to the systematics of Lauxaniidae.

Biology The flight period for this uncommon western and northwestern species begins in mid-June and extends to mid-September. One specimen has been recorded from a light trap at 2,377 m and several from Malaise traps. One specimen was probably attracted to the oozing sap of a cicadellid-infested, western balsam poplar.

Homoneura (Homoneura) knowltoni NEW SPECIES
(Figs. 63, 115)

Knowlton, Harmston & Stains, 1939: 11 [coll. rec. - UT, as *nudifemur*, MISIDENT.].

Diagnosis This medium-sized, clear-winged species is related to the other species of the *setitibia* group, but lacks strong, preapical av F3 bristles.

Discussion Males of *knowltoni* are easily distinguished by the broad, fan-shaped pl S5 processes and the sharply angled and medially directed distal end of the surstylus (Fig. 115). Males of the other species have somewhat foot-shaped pl S5 processes.

Description Total length 3.5-4 mm; wing length 3.5-3.8 mm. Brownish-yellow, with sparse, whitish pollinosity. Similar to *setitibia*, *utahensis*, and *shewelli*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face nearly flat; parafacials approximately ½ plumose. Chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong, well-removed anteriorly from suture; acr with 2 inner rows of weak bristles, 2 incomplete outer rows of setae. Legs yellow, with av F1 ctenidium of 9-11 widely spaced setulae; F3 with weak preapical ad, without preapical av or pv bristles. Wing yellowish, immaculate.

Male: T6 slightly longer than T5, with marginal T6 bristles 1.5 times longer than T5 bristles; pl S5 processes fan-shaped, with 4-5 widely spaced, minute setulae apically; surstylus short, arm-shaped, narrowed ventrally, sharply angled posteriorly, and weakly serrated apically; aedeagus long, tubular, rounded apically; cercus long, linear, basally with dense, short, dorsal setae, apically with longer setae. Female: T7 cylindrical, longer than T6; cercus yellow, with long, black setae.

Types Holotype: ♂, Delta, Millard Co., Utah, VI-19-1968, G. F. Knowlton (USNM 75377). Allotype: ♀, same data as holotype (USNM). Paratypes: 1♂, 1♀, same data as holotype (UTSU); 4♂, 2♀, Ft. Davis, Texas, VI-6-1951, M. R. Wheeler (CNC, UTXA); 7♂, 1♀, Colton, California, VII-5-1951, J. C. Hall (CADA, UCAD); 3♂, 2♀, 8 km sw. Portal, Southwestern Research Station, Arizona, IX-5-25-1965, C. W. Sabrosky, 1,646 m, Malaise trap (USNM).

Specimens examined 86 (50♂, 36♀) from 38 western USA localities:

AR—1♂, Hot Springs, VI-24, H. S. Barber (USNM).

AZ—12♂, 3♀, 7 localities (SEM, UAZ, UCAR, USNM, UTXA); 4♂, 2♀, paratypes.

CA—1♂, 2♀, 3 localities (CADA, UCAR, USNM); 7♂, 2♀, paratypes.

CO—2♂, 6♀, 2 mi (3.2 km) sw. DeBeque, VII-9-1972, R. M. Miller, W. B. Stoltzfus (IASU, RMM).

KS—1♂, Hamilton Co., F. H. Snow, 1,020 m (SEM).

TX—1♀, Big Bend Natl. Pk., V-1959, J. F. McAlpine, oak spring, 1,372 m (CNC); 5♂, 2♀, paratypes.

UT—23♂, 17♀, 22 localities (AMNH, BMNH, CNC, SEM, USNM, UTSU); holotype; allotype; 1♂, 1♀, paratypes.

WY—1♀, Lone Tree, VIII-4-1932, G. F. Knowlton & M. J. James (UTSU).

Remarks This species is named after its collector George F. Knowlton and for his introductory work on the insects of Utah.

Biology The flight period for this common species begins as early as mid-April and extends through September in the southwestern part of its range. Several specimens have been recorded from Malaise traps at elevations from 1,020 to 1,646 m. One specimen has been collected in an ultraviolet light trap, and 1 female was collected from *Yucca brevifolia* (Joshua tree).

Homoneura (Homoneura) setitibia Shewell
(Fig. 113)

Snow, 1903: 219 [coll. rec. - KS, as *tenuispina*, MISIDENT.].

Homoneura praeapicalis Shewell, 1939: 264 [descr. - ALTA, SD; preocc. Malloch, 1925: 320].

setitibia Shewell, 1940: 86 [n. name for *praeapicalis*].

Strickland, 1946: 166 [coll. rec. - ALTA].

Shewell, 1965: 699 [cat., distr. - s. ALTA, SD, KS].

Cole, 1969: 373 [distr. - ALTA].

Diagnosis This small species, having only the crossveins darkened, is closely related to *utahensis* by having a preapical row of 4-6, strong, av F3 bristles. Males have the preapical d T3 bristle 4 times longer than width of T3 at its insertion and females have it slightly longer than the T3, whereas *utahensis* males have the preapical d T3 bristle only 2 times as long and females have it subequal to the width of T3 at its insertion.

Discussion This species has the preapical row of av F3 bristles much longer than *utahensis* and similar to *bakeri*. *H. bakeri* can be distinguished by its weak av F1 ctenidium, whereas *setitibia* has a well-developed ctenidium. Males of *setitibia* have the toe of the foot-shaped p1 S5 processes more pointed than *utahensis* and have a small, ventrally directed spine at the apex of the surstylus, similar to *shewelli* (Figs. 113-114, 116).

Types Holotype: ♂, Lethbridge, Alberta, VI-9-1926, J. E. Revell (CNC 4901). Paratypes: 4♂, Brookings, South Dakota, VI-26-1936, H. C. Severin (CNC, SDSU).

Specimens examined 29 (12♂, 17♀) from 15 central and northwestern NA localities:

ALTA—holotype.

CO—3♀, 3 localities (AMNH, COSU).

IA—1♂, Ledges St. Pk., Boone Co., reared XII-24-1971, R. M. Miller, reared 1972 (RMM).

KS—4♂, 6♀, 3 localities (MCZ, KSSU, SEM, USNM).

NE—2♂, 4♀, 3 localities (IASU, RMM, UNE).

SD—2♀, Vermillion, VI-26-1935, H. C. Severin (SDSU); paratypes.

WY—1♀, nr. Douglas, VII-22-1973, W. B. Stoltzfus (IASU); 1♀, 19.3 km e. Gillette, VIII-29-1962 (UNE).

Biology The flight period for this infrequently collected species begins in late May and extends to late August. One specimen was collected from an ultraviolet light trap, a few from elevations of 1,020 and 1,097 m, and several from sand dunes in Kansas.

One adult was reared from larvae collected in leaf litter, predominantly silver maple *(Acer saccharinum)*, found along the Des Moines River, Iowa, in late December. I suspect that larvae are probably the overwintering stage of this univoltine species.

Homoneura (Homoneura) utahensis NEW SPECIES
(Fig. 114)

Diagnosis This small species, having only the crossveins darkened, is closely related to *setitibia*, but has a weaker preapical row of 4-6, av F3 bristles. Males of *utahensis* also have the preapical d T3 bristle only 2 times as long as the width of T3 at its insertion and females subequal to the width of the T3, whereas *setitibia* males have this bristle 4 times as long as width of the T3 and females subequal to T3 width.

Discussion Males of *utahensis* have the toe of the p1 S5 processes more pointed and surstylus without the apical, ventrally-directed spine, but *setitibia* has the toe more rounded and possesses the spine (Figs. 113, 114). Marginal T5 and T6 bristles are not as strong as those in *setitibia*.

Description Total length 2.75-3.5 mm; wing length 3.3-3.75 mm. Brownish-yellow, with sparse, whitish pollinosity. Similar to *setitibia*.

Frons flat in profile, rounded into facial plane; por equidistant between iv and aor. Face slightly concave; parafacials approximately ½ width of face at middle. Gena about ¼ height of eye. Arista short plumose. Chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong, well-removed anteriorly from suture; acr with 2 inner rows of weak bristles, 2 complete outer rows of setae. Legs yellow, with av F1 ctenidium of 8-11 closely spaced, strong setulae; F3 with a row of 4-6, strong preapical av bristles; preapical d T3 bristle subequal to width of T3 at its insertion. Wing yellowish, with r-m and m darkened.

Male: T6 slightly longer than T5, with marginal T6 bristles only slightly longer than T5 bristles; p1 S5 processes somewhat foot-shaped, with 4-5 widely spaced, minute setulae apically and posteriorly-directed toe pointed; surstylus long, evenly tapering and curved posteriorly to blunt tips, which are minutely serrated apically; aedeagus long, rounded apically, rather spatulate anteriorly; cercus long, with longer setae apically. Female: T7 cylindrical, slightly longer than T6; cercus yellow.

Types Holotype: ♂, Logan, Cache Co., Utah, VII-22-1964, D. W. Davis, ultraviolet light [genitalia preserved in glycerin in microvial] (USNM 75378). Paratypes: 1♂, Pinto, Washington Co., Utah, VIII-5-1965, G. F. Knowlton (UTSU); 1♂, Zion's Canyon, Utah, VI-18-1918 (UTSU); 1♂, Salt Lake City, Utah, VIII-5-1944, Orient. Surv., Peach (USNM); 1♀, Miles City, Montana, VII-22-1915 (UMT).

Biology The only additional collection information about this rarely collected, central western species is that the holotype was collected from an ultraviolet light trap.

Homoneura tenuispina incertae sedis

Homoneura (Homoneura) tenuispina (Loew)
(Figs. 64, 117, 118)

Sapromyza tenuispina Loew, 1861: 349 (Cent. 1, no. 80) [descr. - NE].
Osten Sacken, 1878: 196 [cat., distr. - NE].
Townsend, 1892: 301 [key, distr. - NE].
Lynch Arribālzaga, 1893: 259 [key], 274 [descr. after Loew, 1861].
Snow, 1903: 219 [coll. rec. - KS, = *setitibia*, MISIDENT.].
Aldrich, 1905: 586 [cat., distr. - NE].
Cockerell, 1905: 251 [coll. rec. - KS].
Tucker, 1907: 104 [coll. rec. - KS, CO; CO coll. rec. = *fratercula*, MISIDENT.].
Melander, 1913: 69 [key, distr. - NE, Mexico].
Sapromyza seticauda Malloch, 1914: 32 [key], 34 [descr. - IL]; Pl. II, Fig. 9 [abdomen, ♂], Fig. 12 [wing], Fig. 14 [T3, ♂]. NEW SYNONYMY.
Malloch & McAtee, 1924: 22 [key], 24 [coll. rec. - MD].
Criddle, 1926: 104 [coll. rec. - ONT].
Shewell, 1938: 137 [key], 140 [coll. rec. - ONT].
Strickland, 1938: 205 [coll. rec. - ALTA].
Shewell, 1965: 699 [cat., distr. - s. ALTA, se. Canada, IA, IL, MO, MD, VA].

Remarks Collection records before Malloch (1914) could refer to any of a number of clear-winged species with 1 + 3 dc. Melander (1913) reported this species from Mexico, but I have not located or seen any *Homoneura* species from there.

Diagnosis This medium-sized, clear-winged species is closely related to the *bispina* group in possessing 1 + 3 dc, with the presutural dc strong, well-removed anteriorly from the suture, a facial ridge, usually dark 5th TS3 segments, parafacials ½ the width of the middle of the face and pre-apical av, ad, and pv F3 bristles. However, *tenuispina* differs in having usually immaculate wings (Fig. 64), rather than the r-m and m bordered (Fig. 60), and the gena ¼th the height of the eye, rather than ⅓rd the height.

Discussion Males also possess the following: a fringe of long, weak pv F3 bristles; a fringe of long, conspicuous av T3 bristles on basal half; pl S5 processes large, broadly triangular, setose almost the entire length; pl angles of T7 darkened, with a conspicuous tuft of dense bristles; surstylus small, pointed processes on al angles; gonopods moderately long, slightly curved posteriorly, with small, ventrally-pointed, basal gonopod processes; terminal processes small, slender narrowing distally, with a few conspicuous, black granulations apically and long, fine setae ventrally; cercus small, almost circular (Fig. 117). Females have black cercus, with a few long lateral setae and a concave basal, mesoventral margin (Fig. 118).

Type Holotype: ♂, Nebraska, [C. R. Osten Sacken], H. Loew coll. [head missing] (MCZ 1686).

Remarks Seemingly Malloch (1914) did not check Loew's type when he described *seticauda*, and what he called *tenuispina* is a new species, *mallochi*. According to Malloch's description of *seticauda*, an allotype was supposed to be at the Illinois Natural History Survey. Since Frison (1927) did not list any types, other than the male holotype, and Malloch (1914) did not list any paratypes, the female labeled paratype at the American Museum of Natural History could be the allotype.

Specimens examined 295 (143♂, 152♀) from central and eastern NA localities:

ALTA—1♀, Lethbridge, VI-26-1923, W. Carter, clover blossom (CNC).

AR—1♂, Desha Co., V-10-1971, Kirkton, pecan grove (UAR).

IA—90♂, 75♀, 18 localities (CNC, IASU); 11♂, 15♀, Ledges St. Pk., Boone Co., reared 1972, R. M. Miller (RMM).

IL—24♂, 46♀, 13 localities (AMNH, INHS, USNM, UTXA); ♂, holotype [*seticauda*] (INHS); ♀, "paratype" [*seticauda*] (AMNH).

IN—1♂, Lafayette, VII-4-1914, A. L. Melander (USNM).
KS—6♂, Lawrence, VI-9-1899, H. Kahl (CM); 1♀, Douglas Co., VI, E. S. Tucker (SEM).
KY—3♀, 3 localities (LIM, UKY).
MD—1♂, 1♀, Plummers Is., V-30-1913, R. C. Shannon (USNM).
MO—2♂, 2♀, 2 localities (USNM, UTXA).
NE—1♀, Lincoln, VI-6-1913, G. W. Denning (UNE); holotype.
OH—1♀, Scioto Co., VI-15-1964, P. H. Freytag (UKY); 1♀, Columbus, R. C. Osburn (OHSU).
OK—1♂, Flint, VI-19-1937, Standish-Kaiser (OKSU).
ONT—3♂, 3♀, Ottawa, VII-9-1946, G. E. Shewell (CNC).
QUE—1♀, St. Anne's, VII-31-1923 (AMNH).
VA—1♂, Great Falls, VII-9-1926, J. R. Malloch (USNM).

Biology The flight period of this very common species begins in early May and extends through late August, with most specimens having been collected in June. One male was collected in a pecan *(Carya illinoensis)* grove, 1 male on a tree trunk, and 1 female on a clover *(Trifolium)* blossom. Several specimens were collected from Malaise traps, and many have been collected along rivers and streams.

In late December, 1971, many larvae were collected from leaf litter from along the Des Moines River in Ledges State Park, Iowa. The larvae were feeding on the decaying leaves of silver maple *(Acer saccharinum)*, which were being skeletonized, while leaves of cottonwood *(Populus deltoides)* were not skeletonized. Adults began emerging in late January, but all attempts at laboratory rearing were unsuccessful.

In early June, 1972, many adults were collected from the grass and herbage under young willow *(Salix)* and poplar *(Populus)* along a small stream in Pammel Woods on the Iowa State University Campus at Ames, Iowa. Most adults were observed sitting on the leaves of plants, such as *Galium* (bedstraw) and *Ambrosia artemisiifolia* (common ragweed). While aspirating about 25 specimens into a vial, a sweet smelling odor, somewhat similar to bananas, was noticed, and upon closer examination was coming from the vial of collected *tenuispina*. In the laboratory 5 pairs were placed in a rearing jar and again the odor was detected. This odor was most likely a pheromone as most of the pairs were mating at this time. Some other specimens were sexed and separated, then after a few hours 1 pair each was placed in 4 rearing jars. The following are the observations of the courtship behavior of 1 pair.

The male approached the female and walked around her, without using any noticeable wing or leg displays. Then he faced her and they brushed their antennae together. He quickly turned sideways to her, twisted his abdomen 45 degrees, so the venter faced her, and extended his genitalia. The female remained motionless, except for her antennae moving in the direction of his exposed abdomen and genitalia. This lasted about 20 seconds and then he quickly moved around to her posterior and attempted to mount her. When she resisted, he repeated the previous sequence of events and again mounted her. This time copulation took place and mating lasted for about 5 minutes. The banana-like odor was detectable throughout the courtship, and probably came from some openings just posterior to the last abdominal sternite, which are usually covered by the tip of the aedeagus. Mating positions and behavior were similar to those described for *pernotata*.

Females began laying eggs the day after they were placed in the rearing jars. Some larvae hatched and began feeding on decaying maple leaves, but only a few developed to the 3rd instar and no pupae were formed. One successful rearing was obtained from adults collected in late June, 1972, at Bay's Branch Area, Iowa. Many larvae hatched and began developing on decaying maple leaves, but very few reached the 3rd instar. Only 1 adult emerged in late October.

This species probably has only 1 generation a year because adults have not been collected in September or October. The larvae overwinter among decaying tree leaves.

Homoneura bispina Group

Until Malloch (1914) described more clear-winged *Homoneura*, all earlier collection records referred to Loew's (1861) *bispina* and *tenuispina*. Say's (1829: 177) *Sapromyza connexa* may possibly have been a *Homoneura*, as Melander (1913: 69) stated that *connexa* is probably the female of *bispina*, and Coquillett identified a few specimens of *bispina* as *connexa*. Say's type, however, has been destroyed and, as Malloch (1914: 35) pointed out, a number of species belonging to the various, clear-winged species of the *setitibia*, *bispina*, and *aequalis* groups could fit Say's description, if *connexa* does belong to *Homoneura*. Say's description is brief, and Shewell (1965: 706) listed *connexa* as an unplaced species, questionably in *Homoneura*. If *connexa* belongs to *Homoneura*, the eastern collection records [Fletcher, 1905: 78 (ONT); Johnson, 1910: 798 (NJ); Johnson, 1913: 80 (FL)] probably can be referred to the *bispina* group, and the 1 western record [Baker, 1904: 31 (CA)] probably belongs to *bakeri* or *californica*.

Diagnosis The 5, medium-sized to large species in this group are characterized by the following combination: (1) a slightly produced, broad ridge on lower ⅓rd of face; (2) parafacials ½ width of middle of face; (3) gena ⅓rd height of eye; (4) wing immaculate, except for darkened crossveins; (5) aedeagus with an apical, anteromedial flap; (6) cercus of female small, with basal ⅔rd dark brown or black, dorsally flattened, and with pale yellow, somewhat mesally directed and upturned, pointed apices (Fig. 124).

Discussion Males of this group usually have T3 with long, fine bristles, except *mallochi*, as well as av and pv fringes on the F3 of some of the species. *H. tenuispina* males are very similar to *bispina* males in possessing basal gonopod processes and having the apical, anteromedial flap on the aedeagus (Fig. 121c); however, females of *tenuispina* do not have the flattened cercus. Females of the *bispina* group cannot be readily distinguished at this time by using cercal or genitalic characters.

Key to Species of *bispina* Group

1. ♂ with basal gonopod processes pointed; ♀ with T 7 less than ½ length of T6 2
   ♂ with basal gonopod processes forked; ♀ with T7 at least ½ length of T6 3
2. Apical ⅓rd of 5th TS3 segment dark brown or black (Fig. 88); ♂ without T3 fringes .... *mallochi*, p. 214
   Apices of TS3 at most light brown (Fig. 87); ♂ with pv T3 fringe of fine bristles . *imitatrix*, p. 213
3. ♂ with strong preapical pv F3 fringes; pl S5 processes finger-like, rounded apically (Fig. 122) .. .. *fratercula*, p. 216
   ♂ without or at most with very weak pv F3 bristles; pl S5 processes not as above 4
4. ♂ usually without pv F3 bristles; pl S5 processes triangular, pointed apically (Fig. 123) .... *bispina*, p. 216
   ♂ usually with a weak pv F3 bristle; pl S5 expanding and truncate apically (Fig. 121) .... *truncata*, p. 218

Homoneura (Homoneura) imitatrix (Malloch)
(Figs. 87, 119)

Sapromyza imitatrix Malloch, 1920: 128 [descr. - NJ].
Malloch & McAtee, 1924: 22 [key], 23 [coll. rec. - DC, MD]; Pl. 2, Fig. 28 [genitalia, ♂].
Johnson, 1925a: 256 [coll. rec. - CT].
Hallock & Parker, 1926: 18 [coll. rec. - NJ].
Brimley, 1938: 380 [coll. rec. - NC].
Britton, 1938: 74 [coll. rec. - CT].
Shewell, 1965: 698 [cat., distr. - NJ, CT, s. to LA and FL].

Diagnosis This medium-sized species can be distinguished by having at most only the apices of the 5th TS3 segments light brown (Fig. 87), males with basal gonopod processes pointed and females with T7 shorter than ½ T6.

Discussion Males of *imitatrix* possess a long fringe of fine av and pv F3 bristles, with strong preapical av, pv, and ad F3 bristles, and a fringe of fine pv T3 bristles. This is similar to males of *fratercula*, except *fratercula* does not have the pv F3 fringe extending the entire length of the F3. The male genitalia of *imitatrix* are very similar to *mallochi*, but most noticeably the surstylus is very short, fairly broad, mesoventrally-curved hooks in *imitatrix*, but absent in *mallochi*. *H. imitatrix* also has the pl S5 processes usually twice the width of the gonopods and the apical setae of the cercus evenly spaced (Fig. 119). *H. mallochi* has the pl S5 processes usually equal to the width of the gonopods and the apical setae of the cercus dense (Fig. 120). Females have the cercus usually brown basally, not black.

Types Holotype: ♂, Clementon, New Jersey, V-30-1895, C. W. Johnson (USNM). Allotype: ♀, Anglesca, New Jersey, VII-19-1891, C. W. Johnson (USNM). Paratypes: 1♂, same data as holotype (USNM); 1♂, Riverton, New Jersey, VII-7, C. W. Johnson (USNM); 1♀, DaCosta, New Jersey, VI-4, C. W. Johnson (USNM).

Remarks The paratypes from Riverton and DaCosta, New Jersey, were not labeled; so I have relabeled them.

Specimens examined 56 (34♂, 22♀) from 29 eastern and south central USA localities:

AR—7♂, 4♀, 2 localities (CNC, UAR, USNM).
DC—2♂, 2♀, 2 localities (USNM).
FA—1♀, Monticello, III-20-1919, W. A. Hoffman (USNM); 1♀, Torreya St. Pk., IV-29-1952, O. Peck (CNC).
GA—1♂, Pine Mt., Rabun Co., V-4-1957, W. R. M. Mason (CNC).
IL—3♂, 4♀, 2 localities (INHS).
IN—1♂, Saint Meinrad, Spenser Co., VI-7-1969, G. W. Byers (SEM).
LA—3♂, 3♀, Bossier Parish, V-10-1938, swept from peach (CNC).
MD—1♂, Cabin John, VI-20-1931, A. L. Melander (USNM).
MO—1♀, Lithium, VI-29-1955, M. R. Wheeler (UTXA).
NC—1♂, Herford Co., VI-9-1895, C. W. Johnson (MCZ); 1♂, Pettigrew St. Pk., VI-3-1969, D. A. Young (NCSU).
NE—1♂, Nebraska, C. R. Osten Sacken (MCZ) [syntype of *bispina*, MISIDENT.].
NJ—2♂, 2 localities (ANSP, PADA); types.
NY—1♂, New York, N. Banks (MCZ).
PA—1♂, Swathmore, Delaware Co., VI-2-1912, E. T. Cresson, Jr. (ANSP); 1♂, Swathmore, VI-11-1905 (ANSP).
TX—2♀, College Station, IV-3-1930, J. C. Gaines (CNC); 1♀, College Station, V-11-1935, H. J. Reinhard (CNC); 2♂, 1♀, College Station, VI-1,17-1951, H. J. Reinhard (TXAMU).
VA—4♂, 4 localities (MCZ, OHSU, USNM).

Remarks Johnson (1925a) and Britton (1938) have also reported this species from Connecticut.

Biology The flight period for this uncommon species begins in mid-March in the southern part of its range and extends through mid-July, with most specimens having been collected in May and June. There have been 2 separate collections of a number of specimens from peach *(Prunus persica)*, and 1 male has been collected from soybean *(Glycine max)*. One male from Virginia was labeled "*in coita* on June 4th."

Homoneura (Homoneura) mallochi NEW SPECIES
(Figs. 60, 120)

Sapromyza tenuispina, Malloch, 1914: 32 [key], 36 [descr., coll. rec. - IL], Pl. II, Fig. 10 [S5, ♂]. MISIDENT.
Sanders & Shelford, 1922: 313 [adult ecology - IN].
Malloch & McAtee, 1924: 22 [key], 24 [coll. rec. - VA, MD]; Pl. 2, Fig. 27 [superior forceps, ♂].
Johnson, 1925a: 255 [coll. rec. - NH, MA, RI].
Johnson, 1930: 149 [coll. rec. - MA].
Brimley, 1938: 380 [coll. rec. - NC].
Shewell, 1965: 699 [cat., distr. - NE to NH, s. to TX and NC].

Diagnosis This medium-sized species can be separated by having at least the apical ⅓rd of the 5th TS3 usually dark brown or black, males with short fringes of av and pv F3 bristles and without pv F3 fringes, and females with T7 shorter than ½ T6.

Discussion Male genitalia of *mallochi* are very similar to *imitatrix*, but *mallochi* lacks distinct surstylus, which is evident in *imitatrix*, and the width of the pl S5 processes is usually twice that of the gonopods at the middle in *imitatrix*, but almost equal in *mallochi* (Figs. 119, 120). The medium-sized terminal processes and the long, pointed basal gonopod processes are very similar in both species. Females of *mallochi* and *imitatrix* can be separated by the cercus usually being black basally, not brown as in *imitatrix*.

Description Total length 3-3.5 mm; wing length 3.5-4 mm. Brownish-yellow, with sparse, whitish pollinosity. Similar to *imitatrix*.

Frons slightly swollen in profile, rounded into facial plane; por equidistant between iv and aor, set in narrow, shining plates. Face flat, with a slightly produced, broad ridge on lower ⅓rd; parafacials about ½ width of face at middle. Gena about ⅓rd height of eye. Arista long pubescent. Chaetotaxy: aor slightly shorter than por, ½ iv; por slightly shorter than ov; oc slightly longer than ov; pvt subequal to aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong and well removed from suture; acr with 2 rows of weak bristles. Legs yellow, except apical ⅓rd of 5th TS1, TS2, and especially TS3 segments dark brown or black. F1 av ctenidium of 10-14 closely spaced setulae; F3 with a strong preapical av and ad, occasionally weak pv bristles; males also have a short fringe of weak, fine av and pv bristles. Wing yellowish, with r-m and m darkened and lightly bordered; calypter with light brown, marginal setae distally, before junction of alar lobes.

Male: p1 S5 processes long, rounded apically, with sparse setae, width subequal to gonopod width at middle; T7 twice as long as T6; distinct surstylar extensions absent, with broadly produced lobes on the av and pv angles; terminal processes medium-sized, posteriorly curved, with minute setulae apically and sparse, fine setae ventrally; gonopods long, broadly curving posteriorly, with moderately long, brown, pointed basal gonopod processes; aedeagus large, tubular, bilobed, rounded apically, with an apical, anteromedial flap that covers the distal groove between the lobes; cercus short, with dense apical setae, and concave ventrally. Female: T7 shorter than T6; cercus short, basal ⅔rds dark brown or black, dorsally flattened, with yellow, somewhat mesally directed and upturned, pointed apices, and with some fine, long, weak bristles laterally.

Types Holotype:♂, Potomac River, Fairfax Co., Virginia, VI-7-1955, C. W. Sabrosky (USNM 75379). Allotype: ♀, same data as holotype (USNM). Paratypes: 3♂, 1♀, same data as holotype (USNM); 1♂, 4♀, Odin, Illinois, V-28-1910, in a meadow, C. A. Hart (INHS); 5♂, Springbrook St. Pk., Guthrie Co., Iowa, VI-9-1973, R. M. Miller, W. B. Stoltzfus (CNC, IASU, RMM); 5♂, Cabin John, Maryland, VI-20-1931, A. L. Melander (USNM).

Remarks This species is named for John R. Malloch for his valuable studies of *Homoneura*.

Specimens examined 64 (40♂, 24♀) from 31 north-central and eastern USA localities:

IA—3♂, 2♀, 3 localities (IASU); 5♂, paratypes (CNC, IASU).

IL—3♂, 6♀, 4 localities (INHS, UTXA); 1♂, 4♀, paratypes.

IN—1♂, Saint Meinrad, Spenser Co., VI-7-1969, G. W. Byers (SEM); 1♀, Marion, VII-29-1953, H. D. Stalker (UTXA).

KS—1♂, Baldwin (OHSU).

KY—1♀, Barbourville, V-1-1965, R. E. White (FSCA); 1♂, Louisville, V-25-1953, P. J. Christian (LIM).

MD—2♂, 1♀, 3 localities (USNM); 5♂, paratypes.

MI—1♂, Van Baron Co., VI-11-1949, R. Namba (USNM); 1♀, Little Bear Lake, Grand Junction, VII-15-1914 (INHS).

NC—1♂, 1♀, Willard, V-10-1936, F. S. Blanton (CU); 1♀, Highlands, Macon Co., VI-21-1958, J. L. Laffoon (IASU).

NE—1♂, C. R. Osten Sacken (MCZ).

NY—1♀, Ithaca, VII-13-1917 (INHS).

OH—1♀, Ironton, V-27-1899, J. S. Hine (OHSU); 1♂, Kent, reared 1967, R. M. Miller (RMM).

PA—1♂, Dauphin Co., Hummelstown, V-27-1961, E. U. Balsbaugh, Jr. (PADA).

VA—10♂, 2♀, 2 localities (CNC, IASU, USNM); holotype; allotype; 3♂, 1♀, paratypes.

WV—2♂, Kenova, V-28-1899, J. S. Hine (OHSU).

Remarks Johnson (1925a, 1930) also reported this species from New Hampshire, Massachusetts, and Rhode Island. Shewell's (1965) record from Texas probably refers to *imitatrix*.

Biology The flight period for this uncommon species begins in early May and extends through early August, with most adults having been collected in May and June. In Sanders & Shelford's (1922) study of an Indiana pine-dune animal community, this species was collected in the early morning from shrubs of willow *(Salix)*, dogwood *(Cornus)*, and sandcherry *(Prunus)* on July 13 and August 14.

In early July, 1967, rearing was initiated from a gravid female collected from the herbage in a mesic woods near a seepage area in Kent, Ohio. The female laid only about 25 eggs in the 3 weeks before she escaped. Eggs were deposited singly on and partially in peat moss. Larvae did not readily hatch; so after 4 months some larvae were excised from the chorions. Larvae fed on decaying lettuce and leaves. The 1st instar ranged 6-15 days, 2nd instar 8-13 days, and 12 days for the sole surviving 3rd instar. The prepupal period lasted approximately 48 hours. One male emerged 12 days later and lived 52 days in the laboratory.

This species is probably univoltine with larvae overwintering.

Homoneura (Homoneura) fratercula (Malloch)
(Figs. 88, 122)

Tucker, 1907: 104 [coll. rec. - CO, as *tenuispina*, MISIDENT.].
Sapromyza fratercula Malloch, 1920: 128 [descr. - MT].
Malloch & McAtee, 1924: 22 [key]; Pl. II, Fig. 25 [genitalia, ♂].
Criddle, 1926: 104 [coll. rec. - NS, QUE, ONT, MAN].
Petch & Maltais, 1932: 65 [coll. rec. - QUE].
Shewell, 1965: 698 [cat., distr. - s. to ALTA to s. ONT, s. to NE and GA, as *fraterculus*, ERROR].
Cole, 1969: 373 [distr. - MT, ALTA].

Diagnosis This medium-sized species is distinct in having at least the apical ⅓rd of the 5th TS3 segment usually black and well-developed preapical av, ad, and pv F3 bristles, except pv weak in females. Males also have forked basal gonopod processes and pl S5 finger-like, with rounded apices (Fig. 122); females with the T7 at least ½ length of T6.

Discussion Males also have well-developed apical fringes of av and pv F3 bristles and basal fringes of fine av and pv T3 bristles. They can easily be separated from *bispina* and *truncata*, which lack the pv F3 fringes and at most have a very weak pv F3 bristle.

Types Lectotype: ♂, Powderville, Montana, VI-15-1916, R. Kellogg [genitalia preserved in glycerin in microvial]. Paralectotype: 1♂, same data as lectotype, M. Hanna (INHS).

Remarks The holotype of this species is presumed lost. Therefore I have considered the remaining paratypes as a syntype series of equal status and have designated 1 male as the lectotype.

Specimens examined 75 (51♂, 24♀) from north-central NA localities:

ALTA—1♂, Medicine Hat, ?-14-1956, E. E. Sterns (CNC).
CO—19♂, 11♀, 5 localities (BMNH, COSU, IASU, NMW, SEM).
IA—3♂, 1♀, 4 localities (AMNH, IASU).
IN—1♂, Dunes, VII-19-1933, A. L. Melander (USNM).
KS—1♂, Riley Co., Clearwater, VI-21 (KSSU).
MAN—3♂, 1♀, Awema, V-29-1926, R. D. Bird (CNC).
MI—1♂, 2♀, Marquette, VII-31-1968, G. D. Gill (UNMI).
MN—1♂, Kandiyohi Co., VI-26-1938, H. E. Milliron (UMN).
MT—1♂, 1♀, 2 localities (MTU, UTXA); types.
NE—8♂, 2♀, 5 localities (CNC, IASU, UNE, USNM, UTXA).
ONT—5♂, 6♀, 3 localities (CNC).
SD—4♂, 3 localities (SDSU).
WY—1♂, Platte Co., VIII-9-1950, D. G. Denning (UWY).

Remarks Criddle (1926) reported this species from Nova Scotia, but Shewell (1965) did not include that area in its distribution. I have not examined any specimens from there.

Biology The flight period for this uncommon species begins in early June and extends through mid-September, with the adults having been most commonly collected in June and July. One specimen was collected at 1,219 m in Nebraska. I collected many specimens from a grassy, lowland pasture in Colorado, along with *harti* and *aequalis*.

Homoneura (Homoneura) bispina (Loew)
(Figs. 62, 123, 124)

Sapromyza bispina Loew, 1861: 348 (Cent. 1, no. 79) [descr. - NE].
Osten Sacken, 1878: 196 [cat., dist. - NE].
Townsend, 1892: 301 [key, dist. - NE].
Lynch Arribálzaga, 1893: 263 [key], 294-295 [descr., after Loew (1861)].
Johnson, 1900: 689 [coll. rec. - NJ, as *bispinosa*, error].
Aldrich, 1905: 584 [cat., distr. - NE, NJ].
Johnson, 1910: 798 [coll. rec. - NJ].
Melander, 1913: 69 [key, distr. - MA to KS].
Malloch, 1914: 32 [key], 34-35 [note, coll. rec. - IL], Pl. II, Fig. 11 [S5,].
Gibson, 1915: 143 [coll. rec. - ALTA].
Winn & Beaulieu, 1915: 152 [coll. rec. - QUE, as *bispinosa*, error].
Stewart & Leonard, 1916: 156 [adult ecology - NY].

Malloch & McAtee, 1924: 22 [key], 23 [coll. rec. - MD, VA].
Johnson, 1925a: 255 [coll. rec. - ME, MA, RI, CT].
Johnson, 1925b: 96 [coll. rec. - ME].
Criddle, 1926: 104 [coll. rec. - ALTA].
Johannsen, 1928: 848 [coll. rec. - NY].
Bird, 1930: 435 [adult ecology - MAN].
Petch & Maltais, 1932: 64 [coll. rec. - QUE, as *bispinosa*, error].
Britton, 1938: 74 [coll. rec. - CT].
Shewell, 1938: 137 [key], 139 [coll. rec. - NS, QUE, ONT, MAN, ALTA]; 134 (Pl. 12), Fig. 36 [genitalia, ♂].
Strickland, 1938: 205 [coll. rec. - ALTA].
Adams, 1941: 218, 222, 225 [adult ecology - TN].
Shewell, 1965: 698 [cat., distr. - s. ALTA to NS, s. to KS and NC].
Cole, 1969: 373 [distr. - ALTA].

Diagnosis This large species is distinct in having at least the apical ⅓rd of the 5th TS3 segment usually black and well-developed preapical av and ad, with weak pv F3 bristles, usually absent in males. Males also have forked basal gonopod processes and p1 S5 processes triangular (Fig. 123); females have the T7 at least ½ the length of T6 (Fig. 124).

Discussion This species is generally the largest of the group, having the abdomen slightly longer than the thorax and knob-like terminally in males, elongate and narrow in females. Males have well developed apical fringes of long, fine av F3 bristles and basal fringes of av and pv T3 bristles. They can easily be distinguished from *fratercula*, which has well-developed preapical pv F3 bristles and pv F3 fringe of bristles.

Types Lectotype: ♀, Nebraska, H. Loew coll. [head missing] (MCZ 1678). Paralectotypes: 1♀, Nebraska, H. Loew coll. [head missing] (MCZ 1678); 1♀, Nebraska, H. Loew coll. (CNC 2087).

Remarks Loew's syntype series included 1 male, which belongs to what has been called *imitatrix*. In order to maintain the stability of the name of this very common species, I selected the female in the best condition and the one I suspect to be *bispina*, by its larger size, and designated it as the lectotype. The male was considered to be a misidentified paratype. It must be noted, however, that females of *bispina*, *fratercula*, and *truncata* cannot be distinguished with any degree of certainty at this time.

Specimens examined 800 (387♂, 413♀) from 189 central and eastern NA localities:

ALTA—4♀, Lethbridge, VII-8-1923, H. E. Gray (LEM, UALTA).
CT—1♀, Storrs, VI-6-1931, A. L. Melander (USNM); 1♂, S. Meriden, V-15-1915, H. L. Johnson (BMNH).
DC—1♂, 1♀, Rock Creek Pk., VII-29-1928 (USNM).
IA—123♂, 138♀, 32 localities (AMNH, IASU, UCALA, USNM); 3♂, 3♀, Ledges St. Pk., Boone Co., reared 1971-1972, R. M. Miller (USNM).
IL—89♂, 83♀, 21 localities (AMNH, CM, INHS, USNM).
IN—2♂, 6♀, 5 localities (PC, PU).
KS—1♂, 5♀, 4 localities (OHSU, KSSU, SEM, UAR).
KY—1♀, Louisville, V-29-1954, P. J. Christian (LIM).
MAN—6♂, 8♀, 4 localities (CNC).
MA—3♂, 7♀, 7 localities (CAS, FMNH, FSCA, USNM).
MD—2♂, 6♀, 4 localities (USNM).
MI—13♂, 10♀, 12 localities (CNC, LEM, SEM, UMI, USNM).
MN—8♂, 1♀, 7 localities (IASU, UAR, UMN).
ND—1♂, Fargo, VII-20-1918 (USNM); 1♀, Bismarck, VI-14-1918 (USNM).
NE—2♂, Columbus, VI-14-1940, A. L. Melander (USNM); types.
NJ—16♂, 15♀, 5 localities (AMNH, ANSP, CM, MCZ, USNM).
NS—6♂, 1♀, 2 localities (CNC).
NY—5♂, 12♀, 10 localities (AMNH, CAS, CU, INHS, MCZ).
OH—8♂, 14♀, 8 localities (FSCA, KSU, OHSU); 9♂, 8♀, Kent, reared 1968-1970, R. M. Miller (CNC, RMM, USNM).
OK—2♀, 2 localities (AMNH, OKSU).
ONT—38♂, 27♀, 19 localities (AMNH, CNC, USNM).
PA—10♂, 10♀, 10 localities (ANSP, CM, CU, PADA, USNM, UTXA).

QUE—17♂, 17♀, 8 localities (AMNH, CNC, UM).
SD—12♂, 15♀, 10 localities (IASU, SDSU, UAR).
VA—5♂, 8♀, 3 localities (IASU, USNM).
WI—3♂, 5♀, 7 localities (IASU, INHS, UWI).
WV—3♂, 2♀, 2 localities (CM).

Remarks Collection records of females could be referred to *fratercula*, especially those from the western and central localities. Johnson (1925a) also reported this species from Maine and Rhode Island. Shewell (1965) reported *bispina* south to North Carolina; however, I have seen only 1 female (USNM) from there, and it could easily be *truncata*.

Biology The flight period for this very abundant and widely distributed species begins in mid-May and extends through late August, with most specimens being collected in June and July. One specimen was taken on cottonwood *(Populus deltoides)*, 2 in a *Narcissus* field, 2 from peach *(Prunus persicus)*, 1 from seeding cantaloupe *(Cucumis melo cantalupensis)*, and many from *Iris* and sandbar willow *(Salix interior)*. One specimen was collected from a drainage ditch, many from along rivers.

Stewart & Leonard (1916) used adults of *bispina* in unsuccessful attempts to transmit the bacterium *(Erwinia amylovora)* causing fire blight to apple seedlings. Bird (1930) collected 1 specimen in late August from the herb stratum of a *Salix petiolaris* (a type of willow found in meadows and swales) consocies of an aspen parkland in central Canada. Shewell (1938) reported sweeping adults from reeds *(Phragmites communis)* on river banks with *Camptoprosopella* spp. (Lauxaniidae). Adams (1941) collected *bispina* in the herb stratum of a sugar maple-elm forest from late May to mid-August in Tennessee.

In late December, 1971 a number of larvae, along with larvae of *tenuispina*, were collected in the leaf litter, mainly silver maple *(Acer saccharinum)*, along the Des Moines River in Ledges State Park, Boone Co., Iowa. Males and females began emerging in early February and stopped by mid-February.

During 1968 and 1969, rearings were initiated by use of adults collected from the grass and low herbage in a mesophytic woodland near a small stream at Kent, Ohio. In addition several second and third instars were collected from decaying leaves of red maple *(Acer rubrum)* in early April. One adult emerged in early May and 2 adults emerged in late May. Females usually laid eggs singly or occasionally in clusters of up to 5, averaging 3-5 eggs per day. Most eggs were partially buried in the peat moss, and only some were placed on leaves or twigs. Eclosion took place sporadically and only in a few eggs. Eggs were then transferred to a refrigerator for 3-4 weeks, and they hatched in a few days after being returned to room temperature. The 1st-instar stadium lasted 6-9 days; 2nd, 22-35 days; and 3rd, 17-29 days. The prepupal period was approximately 48 hours, and pupal periods ranged from 11-13 days for both sexes. The preoviposition period for 3 reared females was 20-45 days, with the premating period for 1 female 21 days.

Mating was observed a few times in the laboratory in the late evening, and only 1 lasted for 45 minutes. Mating positions and behavior were similar to those described in *pernotata*. The pairs were fairly active and some were noted to break up easily if disturbed.

Reared males and females lived up to 135 and 126 days, respectively. Field-collected males and females lived 115 days, except 1 male, which lived 150 days. Because of the egg diapause, this species is univoltine, with larvae overwintering.

Homoneura (Homoneura) truncata NEW SPECIES
(Fig. 121)

Diagnosis This medium-sized species may be distinguished by having at least the apical ⅓rd of the 5th TS3 segment usually black and well-developed preapical av and ad, with weak pv F3 bristles. Males also have forked basal gonopod processes, which are yellow, not brown as in *fratercula* and *bispina*, with an anterior lobe on the anterior hooks and p1 S5 processes slightly expanded and truncate apically (Fig. 121); females have the T7 at least ½ the length of T6.

Discussion Males have well-developed apical fringes of long, fine av F3 bristles and basal fringes of av and pv T3 bristles. They can easily be separated from *fratercula*, which has well-developed preapical pv F3 bristles and pv fringe of T3 bristles. Females of *truncata* are not readily separable from *bispina* and *fratercula* at this time.

Description Total length 3-3.5 mm; wing length 3.5-4 mm. Brownish-yellow, with sparse, whitish pollinosity. Similar to *bispina* and *fratercula*.

Frons slightly swollen in profile, rounded into facial plane; por equidistant between iv and aor, set in narrow, shining plates. Face flat, with a slightly produced, broad ridge on lower ⅓rd; parafacials about ½ width of face at middle. Gena about ⅓rd height of eye. Arista short plumose. Chaetotaxy: aor slightly shorter than por, ½ iv, por slightly shorter than ov; oc longer than ov; pvt subequal to aor.

Thoracic chaetotaxy: 1 + 3 dc, presutural dc strong and well removed anteriorly from suture; acr with 2 rows of weak bristles. Legs yellow, except apices of 3rd, 4th, and 5th TS1, TS2, and TS3 segments, which are dark brown or black, especially the apical ⅓rd of 5th TS3. F1 av ctenidium of 14-19 closely spaced setulae; F3 with a strong preapical av and ad, occasionally weak pv bristles, males also have a short fringe of weak, fine av bristles; T3 of males with basal av and pv fringes of fine bristles. Wing yellowish, with r-m and m darkened; calypter with light brown, marginal setae distally, before junction of alar lobes.

Male: pl S5 processes long, expanded, and truncate apically, with sparse setae, twice the width of the gonopods at middle; T7 twice as long as T6; surstylus small, narrow lobes at av angles; terminal processes very small, posteriorly directed, with about 6 small, black setulae apically and some sparse, fine setae dorsally and ventrally; gonopods moderately long, curving posteriorly, with short bifurcate, basal gonopod processes with an anteriorly produced lobe on anterior hook; aedeagus large, tubular, bilobed, rounded apically, with a long, apical anteromedial flap covering the distal groove between the lobes; cercus short, with dense apical setae, and concave ventrally. Female: T7 subequal to T6; cercus short, basal ⅔rds dark brown or black, dorsally flattened, with yellow, somewhat mesally-directed and upturned, pointed apices, and with some fine, long, weak bristles laterally.

Types Holotype: ♂, Lake Junaluska, North Carolina, V-23-1954, H. V. Weems, Jr. (USNM 75380). Allotype: ♀, same data as holotype (USNM). Paratypes: 4♂, same data as holotype (FSCA, RMM); 1♂, 4♀, Highlands, North Carolina, V-9-1957, W. R. M. Mason, Horse Cove, 914 m (CNC); 3♂, Pine Mt., Rabun Co., Georgia, V-15-1951, W. R. M. Mason, 437 m (CNC); 1♂, Ono, Pennsylvania, VI-7-1940, A. L. Melander (USNM).

Biology The flight period for this rarely collected southeastern and central eastern species begins in early May and extends through mid-June, although I suspect adults are probably on the wing through August.

Homoneura cilifera incertae sedis

Homoneura (Homoneura) cilifera (Malloch)
(Figs. 9, 112)

Sapromyza cilifera Malloch, 1914: 32 [key], 33 [descr. - IL]; Pl. II, Fig. 15 [T3,♂].
Malloch & McAtee, 1924: 22 [key], 23 [coll. rec. - MD].
Shewell, 1965: 698 [cat., distr. - IL, MD].

Diagnosis This medium-sized, clear-winged species is characterized by having parafacials ⅓rd width of face at middle and 5th TS3 segment yellow. Males are characterized by having long, fine, irregular fringe of pv F3 bristles, with a conspicuous subbasal bristle and long, fine fringes of av and pv T3 bristles; females are unknown.

Discussion This species is probably closely related to the *aequalis* group in having the parafacials ⅓rd the width of face at middle, but the L3 chaetotaxy of males is more developed, as found in the *bispina* group; the strong presutural dc and presence of pl S5 processes is more characteristic of the *bispina* and *setitibia* groups; and males are somewhat similar to *tenuispina* in having the pl angles of T7 slightly produced.

Males of *cilifera* have the S5 medially divided, somewhat quadrate, with anteromesal margin concave for the reception of the tip of the aedeagus, and with short, finger-like, pl S5 processes, sparsely setose; T7 twice as long as T6; gonopods moderately long, only slightly curved posteriorly, with pointed, mesally directed, basal gonopod processes; surtylus short, mesally curved hooks on av angles; terminal processes large, broadly curving posteriorly, with black granulations and fine setae apically; cercus small, oval, slightly darkened (Fig. 112).

Type Holotype: ♂, Urbana, Illinois, V-24-1888, C. A. Hart, swept from box elder [Acc. No. 14376] (INHS).

Specimens examined 2♂, from 2 middle-eastern USA localities:
IL—1♂, Danvers, V-27-1932, T. H. Frison (INHS); 1♂ type.

Remarks I could not locate the specimen that Malloch & McAtee (1924) reported from Maryland [Plummers Is., V-9-1914], but I believe that it is probably a valid record because of the distinctive males of this species.

Biology This very rarely collected species has only been collected in May, which may be the reason for its seeming scarcity.

Homoneura aequalis Group

Diagnosis This group of 7, medium-sized species, is characterized by the following combination of characters: (1) 1+3 dc or 0+3 dc, increasing in length posteriorly, presutural dc, if present, always closer to anterior postsutural dc than distance between other postsutural dc and close to suture; (2) acr as strong as prsc bristles; (3) parafacials ⅓rd width of middle of face; (4) gena 1/4th-1/5th height of eye; (5) wing immaculate, except for darkened r-m and m; (6) 5th TS3 segment dark dorsally; (7) aedeagus broadly curved ventrally and upturned posteriorly; (8) cercus darkened in both sexes, only apically dark in males.

Discussion This group can be distinguished easily from the *bispina* and *setitibia* groups by the parafacials being ⅓rd rather than ½ width of the middle of face and the presutural dc, if present, close to the suture, not well removed anteriorly, and not as strong as the anterior postsutural dc. Also males of the *aequalis* group lack p1 S5 processes; females are not readily distinguishable by genitalic characters, but some species have the S9 and S10 sometimes partially or completely darkened.

All the new species, except *wheeleri*, were named for the specific different shapes of the terminal processes. These differences may eventually prove to be only variations of a polymorphic species, which could have South Dakota as a common focus. Many more specimens of this rather uncommon group need to be examined, however, to obtain additional variations or series demonstrating character constancy.

Key to Species of *aequalis* Group

1. 1+3 dc, presutural dc as strong as posterior presutural acr; ♂ with ring sclerite yellow 2
   0+3 dc, 1-3 weak presutural dc usually smaller than posterior presutural acr; ring sclerite dark brown 3
2. pv F3 bristles present; terminal processes flattened distally in lateral view, with black granulations apically; ♂ subbasal gonopod processes posteriorly directed (Fig. 12) ...... *aequalis*, p. 220
   pv F3 bristles absent; terminal processes club-shaped distally in lateral view, with black granulations dorsally; basal gonopod processes mesally directed (Fig. 128) .. *clavata*, p. 221
3. Weak apical spots or veins darkened (Fig. 52); ♂ subbasal gonopod processes absent (Fig. 126) ...... *wheeleri*, p. 222
   r-m and m at most darkened (Fig. 61); basal or subbasal gonopod processes present 4
4. ♂ with fine, long, basal pv T3 setae; ♀ with many long, black setae on p1 S8 corners (Fig. 130) ...... *media*, p. 223
   ♂ with only usual appressed setae on T3; ♀ with only usual apical row of long, black setae on S8 5
5. ♂ with defined surstylar extensions; terminal processes flattened apically 6
   ♂ lacking surstylar extensions; terminal processes not flattened apically (Fig. 127) *curva*, p. 223
6. ♂ with terminal processes narrow, spoon-shaped in dorsal view (Fig. 131) ..... *severini*, p. 224
   ♂ with terminal processes broad, fan-shaped in dorsal view (Fig. 132) ...... *flabella*, p. 225

Homoneura (Homoneura) aequalis (Malloch)
(Figs. 7, 125)

Sapromyza aequalis Malloch, 1914: 32 [key]; 36 [descr. - IL].
Malloch & McAtee, 1924: 22 [key, coll. rec. - VA].
Johnson, 1925a: 256 [coll. rec. - VT].
Criddle, 1928: 100 [coll. rec. - MAN, SASK; MAN coll. rec. = *mallochi*, MISIDENT.].
Petch & Maltais, 1932: 65 [coll. rec. - QUE].
Shewell, 1965: 698 [cat., distr. - SASK, SD, NE, VT, VA].
Cole, 1969: 373 [distr. - SASK].

Diagnosis This species can be distinguished by the presence of av, ad, and pv F3 bristles and 1+3 dc, with a strong presutural dc close to the suture. Males have the ring sclerite yellow and apically flattened terminal processes.

Discussion This species is most similar to *clavata*, but males have well-developed and females weak pv F3 bristles, whereas distinct pv bristles are absent in both sexes of *clavata*. Male genitalia of *aequalis* are characterized by the following: aedeagus broadly curved and upturned posteriorly; gonopods slender, with short, apically flattened, posteriorly directed, subbasal processes; ring sclerite not darkened; terminal processes short, sharply elbowed posteriorly in lateral view, flattened apically in dorsal view, with black granulations and some fine setae ventrally (Fig. 125). The terminal processes of *aequalis* are very similar to *severini*, except they are not as expanded apically and lack the thin ventromesal extensions (Fig. 131). Females usually have yellow S9 and 10, which are usually partially brown or black in the other species of the *aequalis* group.

Type Holotype: ♂, Algonquin, Illinois, VII-8-1895, W. A. Nason [genitalia preserved in glycerin in microvial] (INHS).

Remarks Malloch (1914) designated 1 male paratype, which upon dissection, belongs to *curva*.

Specimens examined 93 (42♂, 51♀) from 24 central, north-central and northwestern NA localities:

CO—6♂, 10♀, 9.6 km e. Castle Rock, VII-10-1972, R. M. Miller, W. B. Stoltzfus (IASU); 1♂, Hayden, VIII-8-1965, G. F. Knowlton (UTSU); 10♂, 30♀, 9.6 km e. Castle Rock, reared 1972-73, R. M. Miller (CNC, RMM, USNM).
IA—7♂, Bay's Branch Area, Guthrie Co., VI-29-1972, R. M. Miller, W. B. Stoltzfus (IASU); 2♂, Iowa Lakeside Laboratory, Dickinson Co., VII-18-1959, J. L. Laffoon (IASU).
IL—1♀, Freeport, VII-2-1917 (INHS); 1♀, Chicago, VII-24-1899 (PC); type.
KS—1♂, Riley Co., VII-1-1952, L. O. Warren (UAR).
MN—1♂, se. Houston Co., V-23-1936, H. R. Dodge (UMN).
NE—2♂, Chadron, VIII-2-1950, M. R. Wheeler (UTXA); 2♂, 3♀, 1.6 km s. Hershey, VII-5-1972, W. B. Stoltzfus, R. M. Miller (IASU).
SASK—1♂, Saskatoon, VIII-15-1939, A. R. Brooks [homotype] (CNC); 2♀, Willow Branch, VII-29-1955, A. R. Brooks (CNC).
SD—6♂, 4♀, 9 localities [includes 5 paratypes of *severini*] (AMNH, CNC, SDSU).
UT—1♂, Corinne, VII-1-1915, A. Wetmore (USNM); 1♂, Wanshin, VIII-8-1938, G. F. Knowlton & G. S. Stains (UTSU).
WY—1♂, Ten Sleep, VIII-18-1950, M. R. Wheeler (UTXA); 1♂, Ucross, VII-10-1947, R. E. Pfadt (PU).

Remarks I have not examined any *aequalis* from the east and suspect that Malloch & McAtee's (1924) collection record for Virginia and Johnson's (1925a) collection record for Vermont probably refers to another species in the *aequalis* group, perhaps *curva*.

Biology The flight period for this rather common species begins in late May and extends through late August. In early July, 1972, rearings were initiated by using adults collected from the tall grass in a lowland pasture near Castle Rock, Colorado. Eggs were laid singly on decaying lettuce and tree leaves. Eclosion and larval stadia, especially the 3rd instar, were highly variable. Larvae fed on decaying lettuce and tree leaves. Adults began emerging in the laboratory in mid-November. The premating period for 4 reared females was 8-28 days. Mating was observed 6 times in the laboratory and occurred in the early and late afternoon. Mating postition and behavior were similar to those described in *pernotata*. The pairs remained in 1 place, and mating usually lasted 1 hour.

The preoviposition period for 8 reared females ranged from 7-25 days. The prepupal period lasted 48 hours and the pupal periods for 17 reared adults ranged from 9-13 days. Adults lived 34-115 days in the laboratory.

Three generations were reared in the laboratory, with no indication of diapause. The species is probably at least bivoltine in nature.

Homoneura (Homoneura) clavata NEW SPECIES
(Fig. 128)

Diagnosis This species has 1+3 dc, with a strong presutural dc close to the suture and males with the ring sclerite yellow, as is found in *aequalis*, but can be distinguished by the absence of pv F3 bristles.

Males of *clavata* have the terminal processes somewhat club-shaped distally in lateral view, with black granulations dorsally and sparse, fine setae ventrally; but those in *aequalis* are flattened distally in lateral view, with black granulations apically and some fine setae ventrally. Also *clavata* has mesally directed, pointed, basal gonopod processes, whereas *aequalis* has posteriorly directed, flattened, subbasal processes (Figs. 125, 128).

Discussion The club-shaped terminal processes of *clavata* are unique in the *aequalis* group. Females can be distinguished from other females in the group by the absence of pv F3 bristles.

Description Total length 3.25-3.75 mm; wing length 3.5-4 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *aequalis.*

Frons flat in profile, slight angle with facial plane; por equidistant between iv and aor. Face nearly flat; parafacials about ⅓rd width of face at middle. Gena approximately ¼th height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc = ov; pvt = aor.

Thoracic chaetotaxy: 1+3 dc, presutural dc strong, close to suture; acr with 2 inner rows strong brisltes, 2 outer rows setae, usually complete. Legs yellowish, with av F1 ctenidium of 10-12 closely spaced setulae; F3 with preapical av and ad, without pv bristles. Wing yellowish, with r-m and m darkened.

Male: T6 slightly longer than T5; small, rounded, lobe-like surstylar extension; terminal processes somewhat club-shaped laterally, with black granulations dorsally and sparse, fine setae ventrally; gonopods broad, moderately long, with short, narrow, pointed, mesally directed basal processes; ring sclerite not darkened; aedeagus large, moderately curved ventrally, upturned posteriorly; cercus short, brown apically, with long apical setae. Female: S9 and 10 partially black; cercus black, with long, apical setae.

Types Holotype: ♂, Lake Andes, South Dakota, VI-30-1924, H. C. Severin [genitalia mounted on paper point under specimen] (CNC 15411). Paratypes: 1♂, 3♀, same data as holotype (CNC, SDSU); 1♂, Ottawa, Ontario, VII-19-1946, G. E. Shewell (CNC).

Remarks The holotype and 4 paratypes from South Dakota were originally designated paratypes of *severini* by Shewell (1939).

Biology Nothing is known about the biology of this very rare, north-central species.

Homoneura (Homoneura) wheeleri NEW SPECIES
(Figs. 52, 54, 126)

Diagnosis This species, with partially spotted wings, is readily distinguishable by having at most weak presutural dc and 1-3 additional, weak bristles adjacent to the mp.

Discussion Wings of this species are similar to that of *shewelli,* both having the r-m and m bordered and the apices of R_{2+3}, R_{4+5}, and M_{1+2} clouded, or at least darkened (Figs. 52, 56). However, *shewelli* has a strong presutural dc and the aedeagus is similar to the *aequalis* group, although *wheeleri* does not possess any basal or subbasal gonopod processes (Fig. 126).

Remarks I have also examined 2 females collected from Wyoming [Daniel, VIII-15-1950, M. R. Wheeler (CNC, USNM)], which are very similar to *wheeleri,* except they are conspicuously maculated (Fig. 54) and are slightly larger. This situation may be similar to the wing-spot condition found in some *occidentalis* that have the wing spots weakly developed. Although I suspect that these represent a new species, the collection of a male with well-developed wing spots would help clarify the status of these specimens.

Description Total length 2.75-3.25 mm; wing length 3.2-3.5 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *severini* and *shewelli.*

Frons flat in profile, slight angle with facial plane; por equidistant between iv and aor. Face slightly concave; parafacials about ⅓rd width of face at middle. Gena approximately 1/5th height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc = por and ov; pvt shorter than aor.

Thoracic chaetotaxy: 0+3 dc, 1 or more very weak presutural dc near suture; acr with 2 inner rows strong bristles, 2 outer rows setae, incomplete. Legs yellow, with av F1 ctenidium of 9-12 closely spaced setulae; F3 with preapical av and ad and with very weak pv bristles. Wing yellowish, with r-m and m bordered brown and apices of R_{2+3}, R_{4+5}, and M_{1+2} clouded brown or at least darkened; apical half of ultimate section of M_{1+2} darkened.

Male: surstylar extensions small, mesally directed processes at av angles; terminal processes somewhat foot-shaped laterally, scoop-shaped and flattened dorsally, with black granulations apically, fine setae ventrally, and small, apically, flattened, posteriorly directed, subbasal processes; gonopods narrow, moderately long, evenly curved posteriorly, without subbasal processes; aedeagus large, broadly curved ventrally, upturned posteriorly; cercus short, brown and with short, dense, apical setae. Female: cercus black, with long, apical setae.

Types Holotype: ♂, Slide Lake, Wyoming, VIII-14-1951, M. R. Wheeler [genitalia preserved in glycerin in microvial] (USNM 75381). Allotype: ♀, Kemmerer, Wyoming, VIII-14-1950, M. R. Wheeler (USNM). Paratypes: 1♂, same data as holotype (UTXA); 2♂, 1♀, State Bridge, nr. Bond, Colorado, VI-24-25-1961, C. H. Mann, elevation 2,133 m, dry river bed and bank (CNC); 1♂, Delaney Lakes, w. Walden, Jackson Co., Colorado, VIII-13-1968, P. H. Freytag, on *Salix* (RMM).

Remarks This species is named for its collector, the noted dipterist, Marshall R. Wheeler.

Biology The biological data for this rarely collected species indicate that it is found at moderate elevations near water sources and associated with willows.

Homoneura (Homoneura) media NEW SPECIES
(Figs. 129, 130)

Diagnosis This species is distinguished by having 0 + 3 dc, with 1-2 weak presuturals shorter than posterior presutural acr. Males can be distinguished by the long, basal, pv T3 setae, females by the many, long, black setae on the pl corners of S8 (Fig. 130).

Discussion The terminal processes are expanded and flattened apically and scoop-shaped (Fig. 129), a condition intermediate to the spoon-shaped processes of *severini* and fan-shaped processes of *flabella*.

Description Total length 3-3.5 mm; wing length 3.3-3.6 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *severini* and *flabella*.

Frons flat in profile, slight angle with facial plane; por equidistant between iv and aor. Face nearly flat; parafacials about ⅓rd width of face at middle. Gena approximately ¼th height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc = ov; pvt = aor.

Thoracic chaetotaxy: 0 + 3 dc, with 1-2 very weak presutural dc less than length of presutural acr; acr with 2 inner rows strong bristles, 2 outer rows of setae. Legs yellow, with av F1 ctenidium of 10-13 closely spaced setulae; F3 with preapical av, ad, and pv bristles; T3 of male with some longer, basal pv setae. Wing yellowish, with r-m and m darkened.

Male: small, lobe-like surstylar extensions on al and pl corners; terminal processes large, flattened, posteriorly curved, with apical, black granulations and fine, ventral setae, slightly expanded apically in dorsal view; gonopods broad, moderately long, with long, narrow, posteriorly directed subbasal processes; ring sclerite darkened; aedeagus large, broadly curved ventrally, upturned posteriorly but not pointed apically; cercus short, apically brown setae. Female: S8 with dense, long setae, in 2 or more marginal rows on the pl corners; S9 and 10 slightly darkened apically; cercus dark, with long, apical setae.

Types Holotype: ♂, Whiterocks, Duchesne Co., Utah, VII-11-1972, W. J. Hanson & G. F. Knowlton [genitalia preserved in glycerin in microvial] (USNM 75382). Allotype: ♀, same data as holotype (USNM). Paratypes: 1♀, Cache Co., Blacksmith Fork Canyon, Utah, VII-11-14-1964, W. J. Hanson, Malaise trap (UTSU); 1♀, Cache Co., Blacksmith Fork Canyon, Utah, VII-26-1972, G. F. Knowlton (UTSU); 1♀, Duchesne, Utah, IX-3-1937, G. F. Knowlton & F. C. Harmston, in meadow (UTSU); 1♀, 6.4 km s. Manila, Daggett Co., Utah, VIII-18-1963, N. & B. Marston (KSSU); 1♂, 9.6 km s. Castle Rock, Colorado, VII-10-1972, R. M. Miller (RMM); 1♂, Elk Point, South Dakota, VI-20-1924, H. C. Severin [paratype of *severini*] (SDSU); 1♂, Elk Point, South Dakota, VI-12-1925, H. C. Severin [paratype of *severini*] (SDSU); 1♂, Carbon Co., Wyoming (CNC).

Biology The flight period for this very uncommon, central-western species begins early in June and extends through early September. One female has been collected in a Malaise trap and 1 in a meadow.

Homoneura (Homoneura) curva NEW SPECIES
(Figs. 61, 127)

Diagnosis This species can be distinguished by having 0+3 dc, with 1-2 weak presutural dc shorter than posterior presutural acr; males with the terminal processes long and broadly curved upward distally, not dorsoventrally flattened, lacking surstylar extensions (Fig. 127). Females are not readily distinguishable from *severini* and *flabella*.

Discussion In males of *curva*, the short, narrow, posteriorly-directed basal gonopod processes are somewhat similar to those of *severini* (Figs. 127, 131).

Description Total length 3-3.5 mm; wing length 3.3-3.5 mm. Brownish-yellow, with whitish pollinosity laterally and ventrally. Similar to *severini*.

Frons flat in profile, slight angle with facial plane; por equidistant between iv and aor. Face nearly flat; parafacials about ⅓rd width of face at middle. Gena approximately 1/5th height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc = ov; pvt = aor.

Thoracic chaetotaxy: 0 + 3 dc, with 1 or 2 very weak presuturals less than length of presutural acr; acr with 2 inner rows strong bristles, 2 outer rows setae, usually complete. Legs yellow, with av F1 ctenidium of 12-14 closely spaced setulae; F3 with preapical av, ad, and pv bristles. Wing yellowish, with r-m and m darkened.

Male: without surstylar extensions; terminal processes long, broadly curved upward, with black granulations apically and sparse, fine setae ventrally; gonopods broad, moderately long, with short, narrow, posteriorly directed basal processes; ring sclerite black; aedeagus large, broadly curved ventrally, upturned posteriorly; cercus short, apically brown, with long apical setae. Female: cercus black, with long, apical setae.

Types Holotype: ♂, Mica, Washington, VII-14-1918, A. L. Melander (USNM 75383). Paratypes: 3♂, same data as holotype (USNM); 1♂, Urbana, Illinois, VI-28-1889, C. A. Hart [paratype of *aequalis*] [Hart 514] (INHS); 7♂, Ottawa, Ontario, VII-18-19-1946, G. E. Shewell (CNC).

Specimens examined 23 (21♂, 2♀) from 12 northwestern and north-central NA localities:

ALTA—1♂, 1♀, Macleod, IX-2-1928, O. Bryant (CAS); 1♂, Lethbridge, VII-28-1923, H. E. Gray (UALTA).

BC—1♂, Swan Lake, VII-29-1917, A. L. Melander (USNM).

IA—1♂, 1♀, Pilot Mound St. For., Boone Co., VIII-30-1971, R. M. Miller (IASU); 1♂, Bay's Branch Area, Guthrie Co., reared VI-9-1973, R. M. Miller (RMM).

ID—1♂, Chatcolet, VIII-1915, A. L. Melander (USNM).

IL—1♂, Urbana, VI-20-1915 (INHS); 1♂, paratype.

MAN—1♂, Transcona, VII-26-1927, C. S. Brooks [paratype of *severini*] (CNC).

ONT—7♂, paratypes.

SD—1♂, Yankton, VI-21-1924, H. C. Severin [paratype of *severini*] (SDSU).

WA—holotype; paratypes.

Biology The flight period for this uncommon, northern species begins early in June and extends through early September. One male emerged in late June from decaying leaves of silver maple (*Acer saccharinum*) and cottonwood (*Populus deltoides*) collected in early June, 1971, from a low wet area at Bay's Branch Area, Iowa.

Homoneura (Homoneura) severini Shewell
(Fig. 131)

Homoneura severini Shewell, 1939: 265-266 [descr. - NWT, BC, MAN, SD].

Shewell, 1965 [cat., distr. - NWT, s. AK and YT to n. MAN, s. to UT, MN, and s. ONT].

Cole, 1969: 373 [distr. - AK, UT].

Griffiths, 1972: 94 [note - examined genitalia, ♂].

Diagnosis This species is characterized by having 0 + 3 dc, with 1-3 usually weak presutural dc shorter than posterior presutural acr. Males can be distinguished by the terminal processes being narrow and spoon-shaped apically (Fig. 131).

Discussion The terminal processes of *severini* are not as expanded apically as *media* or *flabella*, with black granulations and flattened apically, with fine, black setae ventrally. The surstyli are ventral lobes, curving mesally. Gonopods are rather small, with short, narrow, posteriorly directed subbasal processes (Fig. 131).

In Griffiths' (1972) study of lauxaniid genitalia, he stated that the aedeagus is small or apparently absent in some groups (e.g., *Celyphus*, *Homoneura*). In most of the Nearctic and Palaearctic species that I have examined, including *severini*, which Griffiths stated he examined, the aedeagus is usually well developed.

Types Holotype: ♂, Cameron Bay, Great Bear Lake, Northwest Territories, VII-22-1937, T. N. Freeman (CNC 4903). Allotype: ♀, same locality as holotype, VII-12-1937, T. N. Freeman (CNC). Paratype: 1♂, 1♀, Fairmont, BC, VII-28-1926, A. A. Dennys (CNC).

Remarks The remaining 14 paratypes originally designated by Shewell (1939) belong to *aequalis*, *clavata*, *curva*, and *media*.

Specimens examined 23 (13♂, 10♀) from 13 north-central and northwestern NA localities:

AK—2♀, Camp 327, Alaskan Eng. Comm., J. M. Aldrich (USNM).

ALTA—7♂, 5♀, 5 localities (CAS, CNC).

BC—1♂, Loon Lake, Selkirk Mts., VII-14-1908, J. C. Bradley (CU); 1♂, Toad R. Lodge, Alaska Hwy., VII-20-1969, E. E. MacDougall, 1373 m (CNC); paratypes.

MAN—1♂, Eastern Cr. nr. Churchill, VII-9-1952, J. G. Chillcott (CNC).

NWT—holotype; allotype.

SASK—1♂, Christopher Lake, VII-8-1959, A & J Brooks (CNC).

YT—1♀, 22.5 km e. Dawson, 396 m, VIII-3-1962, P. J. Skitsko (CNC).

Biology The flight period for this uncommon species begins early in July and extends through mid-August. A few specimens have been collected at elevations of 396 to 1,829 m. One specimen was collected in a meadow and 1 from a Malaise trap.

Homoneura (Homoneura) flabella NEW SPECIES
(Fig. 132)

Diagnosis This species is distinguished by having 0+3 dc, with 1-2 weak presutural dc shorter than posterior presutural acr; males with terminal processes being broad and fan-shaped apically (Fig. 132).

Discussion The terminal processes of *flabella* are the greatest expanded (together as wide as the epandrium) of all the species of the *aequalis* group and closely resemble *media* and *severini*. *H. media* has the terminal processes somewhat smaller, scoop-shaped, and lacks surstylar extensions, whereas *severini* has the terminal processes smaller, spoon-shaped, and possesses ventral surstylar extensions, as does *flabella* (Figs. 130-132).

Description Total length 3-3.5 mm; wing length 3.3-3.6 mm. Brownish-yellow with whitish pollinosity laterally and ventrally. Similar to *media* and *severini*.

Frons flat in profile, slight angle with facial plane; por equidistant between iv and aor, set in narrow, shining plates. Parafacials about ⅓rd width of face at middle. Gena approximately ¼th height of eye. Arista long pubescent. Chaetotaxy: aor shorter than por, ½ iv; oc = ov; pvt = aor.

Thoracic chaetotaxy: 0+3 dc, with 1-3 very weak presutural dc less than length of presutural acr; acr with 2 inner rows strong bristles, 2 outer rows setae, usually complete. Legs yellow, with av F1 ctenidium of 7-14 closely spaced setulae; F3 with preapical av, ad, and pv bristles. Wing yellowish, with r-m and m darkened.

Male: surstyli large, ventral lobes, curving mesally and small pointed processes at pl corners; terminal processes large, flattened, posteriorly curving, with ventroapical, black granulations and fine ventral setae, fan-shaped in dorsal view; gonopods broad, moderately long, with long, narrow, posteriorly directed subbasal processes; ring sclerite darkened; aedeagus large, broadly curved ventrally, upturned posteriorly; cercus short, apically with black setae. Female: S9 and 10 at least partially darkened; cercus, dark, with long, apical setae.

Types Holotype: ♂, Ottawa, Ontario, VII-19-1946, G. E. Shewell (CNC 15412). Paratypes: 10♂, same data as holotype (CNC, USNM); 3♂, 1♀, Ninette, Manitoba, VI-14-1958, J. F. McAlpine, ex *Salix* sp. (CNC); 2♂, 1♀, Great Deer, Saskatchewan, IX-18-1948, J. R. Vockeroth (CNC).

Specimens examined 11 (9♂, 2♀) from 6 northern CAN localities:

ALTA—1♂, Pincher, VII-10-1941, E. H. Strickland (UALTA); 1♂, 24.1 km e. Morley, VIII-10-1962, K. C. Herrmann (CNC).

MAN—3♂, 1♀, paratypes.

ONT—holotype; 10♂, paratypes.

QUE—1♂, New Richmond, VIII-6-1954, J. E. H. Martin (CNC).

SASK—2♂, 1♀, paratypes.

Biology The flight period of this very uncommon species begins in mid-June and extends through mid-September.

ECOLOGY OF NEARCTIC HOMONEURA

Following is a discussion of the generalized ecology of 17 species, based on the biological observations and rearings conducted at Kent, Ohio, 1967-1969, and at Ames, Iowa, 1971-1975. Also included are the only 2 previously reported rearing records of *americana* (Miller & Foote, 1975) and *trochantera* (McDonald, Heed, & Miranda, 1974) (Table 1).

The flight period for most species begins in late May and may extend through October, with specimens being most commonly collected in June and July. Courtship behavior has been observed and described in only 1 species, *tenuispina*, which evidently has a pheromone associated with it. The premating period of several species has been recorded and extends 8-36 days after emergence of the female. Mating in nature and in the laboratory has been noted and described for several species. It occurred in morning, late afternoon, and early evening and lasted 5 minutes to a few hours. The mating position and behavior were similar to those described for *pernotata*.

The preoviposition period ranged from 7-52 days. Eggs were usually deposited singly, occasionally in clusters of up to 5, on and in moist peat moss and underneath and between decaying tree leaves in the late afternoon and early evening. Fecundity varied greatly with the individual, but there is at least a potential of laying up to 10 eggs daily and 600 eggs during the female's egg-laying period. The incubation period varied from 2 days to several weeks or more, probably because of genetic variability or a weak diapause. In 1 species, *bispina*, a rather strong diapause was indicated, which could be broken by exposing the eggs to cold temperatures for a few weeks. Hatching in nature may be stimulated by the cool, fall temperatures, which also trigger leaf fall and provide new food for the larvae.

The 1st instars fed on decaying lettuce *(Lactuca sativa)* and mined the epidermal layers of decaying tree leaves. Second instars continued to mine leaves; 3rd instars were more commonly found between decaying leaves, skeletonizing them. Larval stadia were highly variable, with the total larval period lasting 15-101 or more days.

Larvae of *Homoneura* exhibit the primitive compost-feeding habit (Oldroyd, 1964); however, they are specialized in mining and feeding on decaying fallen leaves, with the possible exception of *harti*, which seems to have habits more similar to the ancestral vegetable debris feeder. Although most larvae can be considered true leaf miners, they are a specialized saprophytic group and not phytophagous (Hering, 1951). Moreover, Miller & Foote (1975) suggested the possibility that the larvae may be utilizing yeasts, fungi, and bacteria. Larvae have been collected and reared from the decaying leaves of 7 genera of 5 plant families: Aceraceae *(Acer saccharum, A. saccharinum, A. rubrum)*; Compositae *(Hieracium californica, Cynara venosum, C. scolymus)*; *Corylaceae (Alnus* sp); Lauraceae *(Sassafras albidum, Umbellularia californica)*; Rosaceae *(Prunus serotina)*. Miller & Foote (1975) reported that larvae of *americana* preferred decaying leaves of maple and cherry over alder, elm, oak, and beech. In nature the overwintering stage is the quiescent larva, and field-collected larvae are mainly from leaves of *Acer saccharum* and *saccharinum* (sugar and silver maples, respectively).

Pupariation takes place in the late spring, often within the mined, decaying leaves. The prepupal period lasts approximately 48 hours, and pupal period ranges from 10-16 days, with males sometimes emerging 1 day before the females. A number of pupal parasitoids were reared from field-collected larvae of at least 5 undetermined species of *Homoneura* in Ohio: 2♀, *Kleidotoma (Tetrarphoptra)* sp., 15♀, *Glauraspidia* sp., and 19♂, *Rhoptromeris* sp. (Hymenoptera: Cynipidae). Three newly emerged pairs of *Glauraspidia* females and *Rhoptromeris* males were observed *in copula* and Burks (pers. com.) was satisfied that they belong together and called them *Glauraspidia*.

Adults collected early in the season lived 2-4 months in the laboratory; reared adults, 1-3 months. Most species have 1 generation per year with probably a partial 2nd generation; more generations per year are more common in the southern parts of a species' range.

Ecological studies on the adults of 10 named, eastern species have been conducted, with species having been collected mainly from the herb and occasionally the shrub and tree strata of mesophytic, deciduous forests (Table 2). One species, *sheldoni*, is evidently associated with plants of sphagnum bogs (Blake, 1927; Judd, 1960). At certain times in late spring and early summer, *Homoneura* adults can be very common in some areas, especially near swamps and along streams. Adults can be found sitting on the undersides of low vegetation and in leaf litter in early morning and evening; in late afternoon they are active and commonly seen on the upper surfaces of the leaves.

Cole (1969) listed 11 species with western distribution, but only 1, *occidentalis*, is restricted to west of the Rocky Mountains. Many of the new species are from the west, which now has 9 more

Table 1. Life-cycle data for 19 species of *Homoneura*.

Species	Larval Microhabitat	Larval Food (decaying)	Premat. Period (days)	Preovip. Period (days)	Incub. Period (days)	Larval Period (days)	Pupal Period (days)	No. Gen. per Year	Rearing Record (state)
aequalis	ND[a]	lettuce & leaves	8-28	7-25	ND	ND	9-13	2+	CO
aldrichi	ND	lettuce & leaves	ND	ND	ND	ND	ND	1	IA
americana	rotting(?) vegetation	*Hieracium venosum*	ND	ND	ND	ND	ND	ND	NY
	leaf litter	*Sassafras albidum*	ND	23-35	2-22+	15-65+	10-13	2	OH
		Acer saccharum							
		Prunus serotina							
birdi	leaf litter	*Acer saccharinum*	13	13-25	ND	ND	10-12	1	IA
		Prunus serotina							
bispina	leaf liffer	*Acer saccharinum*	ND	ND	ND	ND	ND	ND	IA
	leaf litter	*Acer rubrum*	21	20-45	Diapause	45-73+	11-13	1	OH
citreifrons	ND	lettuce & leaves	ND	ND	7+	ND	ND	1	OH
curva	leaf litter	leaves	ND	ND	ND	ND	ND	1	IA
fraterna	leaf litter	*Acer rubrum*	ND	ND	ND	ND	13	ND	OH
		and *saccharum*							
	leaf litter	*Acer saccharum*	ND	20	ND	ND	14-15	1	IA
fuscibasis	leaf litter	*Acer rubrum*	ND	ND	ND	ND	ND	1	OH,IA
		Acer saccharum							
harti	ND	lettuce & leaves	ND	32-45	ND	85	14-16	1-½	CO
incerta	leaf litter	*Sassafras albidum*	ND	24-26	ND	ND	10	1	OH,IA
		Acer rubrum							
		Acer saccharum							
mallochi	ND	lettuce & leaves	ND	ND	26-40+	8	12	1	OH
nubila	rotting vegetation	*Cynara scolymus*	ND	ND	ND	ND	ND	ND	MO
	ND	lettuce & leaves	ND	17-30	ND	ND	11-15	1-½	KS,IA
nubilifera	ND	lettuce & leaves	ND	ND	ND	ND	10-14	1-½	IA
pernotata	leaf litter	*Acer saccharum*	10-25	16-40	3-16+	44-101+	10-14	1+	OH
		Alnus sp.							
philadelphica	leaf litter	*Acer rubrum*	10-36	12-52	3-13+	18-49+	10-13	1-½	OH,IA
		Alnus sp.							
		Acer saccharum							
setitibia	leaf litter	leaves	ND	ND	ND	ND	ND	1	IA
tenuispina	leaf litter	*Acer saccharinum*	ND	ND	ND	ND	ND	1	IA
trochantera	leaf litter	*Umbellularia californica*	ND	ND	ND	ND	ND	1	CA

[a] ND = not determined.

Table 2. Adult ecological studies of *Homoneura*.

Species	Strata	Stand	State	Reference
americana [*compedita*]	herb	white oak-shagbark hickory	MO	Dowdy (1947)
	herb-low shrub, high shrub-low tree	red oak-pignut hickory	TN	[a] Whittaker (1952)
birdi [as *pernotata*]	herb, shrub, tree	cottonwood	MAN	Bird (1930)
bispina	herb	willow	MAN	Bird (1930)
	herb, shrub, tree	sugar maple-American elm	TN	[a] Whittaker (1952)
conjuncta	herb?	red oak-sugar maple	IL	Smith (1928)
fraterna	herb	American elm-sugar maple	IL	Weese (1925)
	herb, shrub-low tree	gray beech	TN	[a] Whittaker (1952)
incerta	tree	white oak-shagbark hickory	MO	Dowdy (1947)
	herb	sugar maple-American elm	IL	Jones (1946); Shelford (1951)
	herb, shrub-low tree, herb-low shrub	gray beech	TN	[a] Whittaker (1952)
	high shrub-low tree	red oak-pignut hickory	TN	[a] Whittaker (1952)
	shrub, herb	table-mountain pine heath	TN	[a] Whittaker (1952)
lamellata [*deceptor*]	tree-top	cottonwood	MAN	Bird (1930)
mallochi [as *tenuispina*]	shrub	Jack pine-willow	IN	Sanders & Shelford (1922)
ornatipes	shrub, herb	table-mountain pine heath	TN	[a] Whittaker (1952)
philadelphica	herb	oak-hickory, beech-maple	IL	Shelford (1913)
	herb	American elm-sugar maple	IL	Weese (1925); Shelford (1951)
	herb?	red oak-sugar maple	IL	Smith (1928); Smith-Davidson (1932)
	herb	eastern hemlock	TN	[a] Whittaker (1952)
	herb, shrub-low tree	gray beech	TN	[a] Whittaker (1952)
	shrub, herb	mixed mesophytic	TN	[a] Whittaker (1952)

[a] Species records unpublished.

species, many of which are known from only a few specimens. Some collection records of isolated females probably represent new species. Probably additional species will be found in the west, which has not been intensively collected and the collection of specimens depends on being in the right place at the right time of year. Furthermore, Cole stated that endemic species of Diptera can be found in each of the western states, and perhaps relatively more of these local forms in California, where many barriers would have isolated them during past ages, or where there are distinctive habitats, such as sand dunes along the Pacific Ocean coastline.

The Nearctic species can be divided into 2 large groups with some common morphological characters that can be somewhat correlated to habitat. The basically eastern and northern species of *Tarsohomoneura; conjuncta, philadelphica* and the *incerta, fraterna, nubilia,* and *aequalis* groups have large eyes (gena-eye height: 1/4th-1/6th, narrow parafacials (parafacial-face width: ⅓rd), and males without posterolateral sternite 5 processes. One major group is usually associated with the eastern temperate deciduous and northern boreal forests. Furthermore, most species have maculated wings, which perhaps is an adaptation to shaded habitats, as large eyes might be to help increase vision. Usually the more heavily patterned species are found in darker forests, while species with only the crossveins spotted are found in the lighter ecotones and successional zones of grass and deciduous trees.

The other major group is generally western and characterized by having wide parafacials (parafacial-face-width: ½-⅔rds), males possessing posterolateral sternite 5 processes, and usually small eyes (gena-eye height: ½-¼th). Only the species of the *trochantera* and *occidentalis* groups, along with *lamellata,* are the exceptions by having large eyes (1/4th-1/5th); most of these species have patterned wings and are probably associated with more shaded habitats. The rest of the species in this group have, at most, darkened crossveins or very weak apical spots: *tenuispina, bakeri, setula, inaequalis, littoralis* and the *bispina, setitibia,* and *harti* groups. Only some species of the *bispina* group and *harti* and *littoralis* seem to be basically eastern, but their ranges extend westward into the Great Plains of central North America. These species are found quite commonly on the periphery of woodlands near streams and some are associated with sand dunes. They also appear to be more active fliers than the rather sluggish species found in the more shaded, wooded habitats. The possession of small eyes is evidently correlated directly to the widened parafacials and the frons being slightly to distinctly swollen anteriorly. The reduced wing maculation is probably a selective adaptation, making species living in open habitats less obvious to potential predators, while maculations on wings could serve to break up the conspicuous yellowish wings of species in shaded habitats. Cole (1969) pointed out that western species of Diptera are, in some instances, related to North and Central European forms. *H. occidentalis* and *arizonensis* seem to be closely related to the Holarctic *lamellata,* as so might be *trochantera.*

The only species, besides the obviously different, introduced, oriental *unguiculata,* that do not fit into either of the major groups are *citreifrons* and *cilifera. H. citreifrons* is closer to the eastern group by the males lacking posterolateral sternite 5 processes, but has generally small eyes (¼th), swollen frons, and wide parafacials (½), especially in the males. *H. cilifera* possesses the posterolateral sternite 5 processes, generally small eyes ¼th), but has narrow parafacials (⅓rd).

Sexual dimorphism occurs in a number of species: in the subgenus *Mallochomyza,* males of *citreifrons* have larger heads, longer, paler bristles, and fainter wing patterns than the females. In the subgenus *Tarsohomoneura,* males of all the species, except *sheldoni,* have at least the 2nd hindtarsal segments dilated and black and in *ornatipes* and *melanderi* also are highly ornamented with long, clavate bristles. Females have the corresponding segments black but not dilated or ornamented. In the subgenus *Homoneura,* males of many species exhibit increased length and development of setae and bristles on the hindfemora, hindtibiae, and hindtarsi. This occurs mainly in the *nubila, setitibia,* and *bispina* groups and a few of the ungrouped species, such as *bakeri* and *cilifera.* Also males of *inaequalis* and *setula* have the setae usually found on the venter of the hindtrochanters strongly developed as setulae. This condition is most developed in *littoralis,* which also has many setulae on the basal half of the venter of the hindfemora. When the male is in mating position, these setulae are placed against the dorsum and sides of the female's abdomen and probably enable the male to hold firmly onto the female in the open habitats and shorelines of ponds and lakes where this species occurs. Males of the *harti* group have the anterior midtibial claw enlarged and slightly recurved. This claw is hooked on the base of the female's wing during mating and probably helps the male remain mounted in the relatively unprotected sand dune and open grassland habitats occupied by members of this group.

A number of these dimorphic characters are obviously functional and correlated with certain habitats, while others are evidently sensory, functioning in attracting the female. This is most likely true in the males of most *Tarsohomoneura* species that have black, enlarged, and sometimes ornamental tarsomeres. Probably certain other morphological characters are correlated to particular habitats. Further ecological relationships to specific habitats for other species, especially the western ones, await more detailed observations. Moreover, additional larval rearing information would be invaluable in determining the exact ecological role of *Homoneura*.

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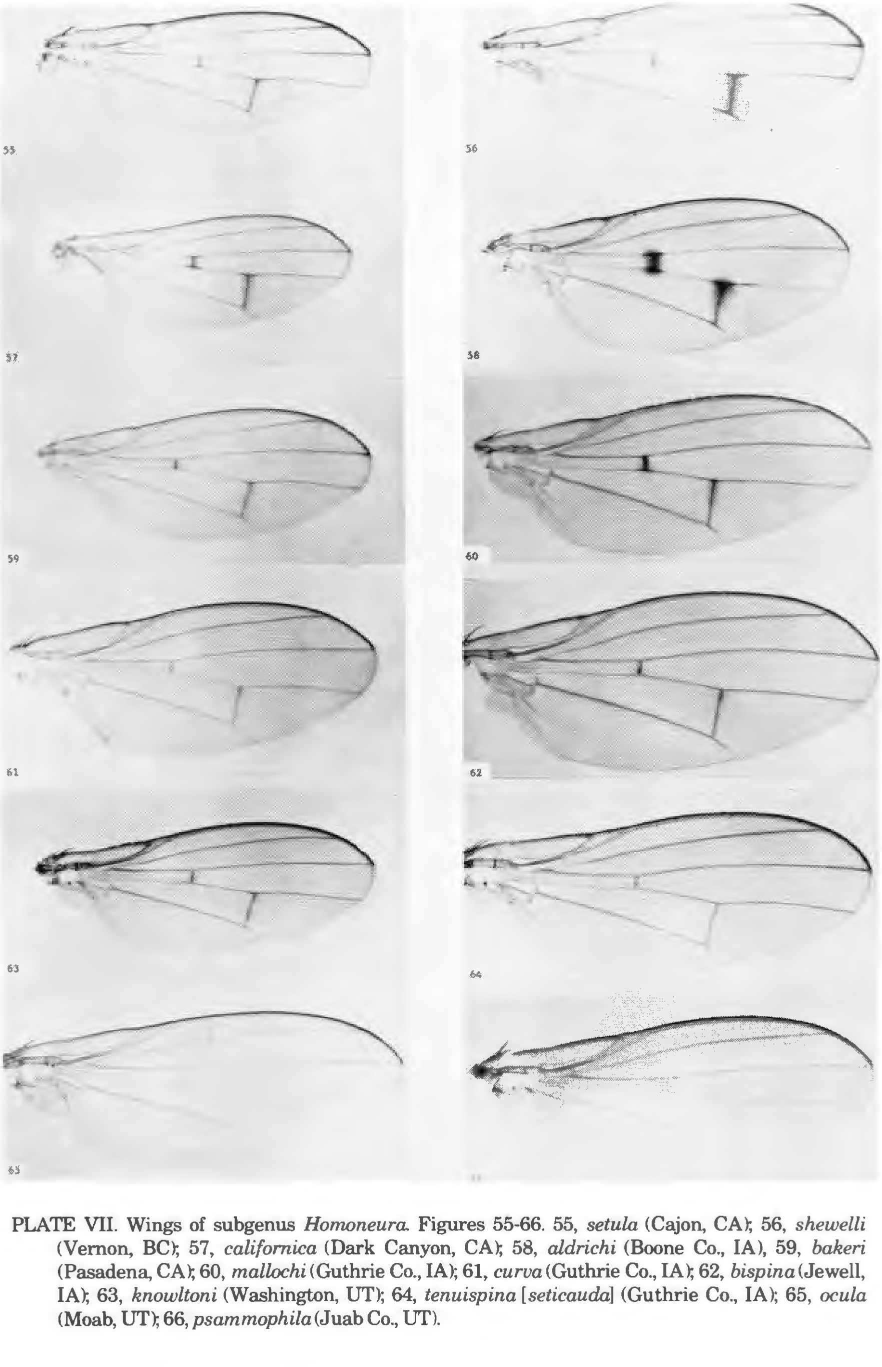

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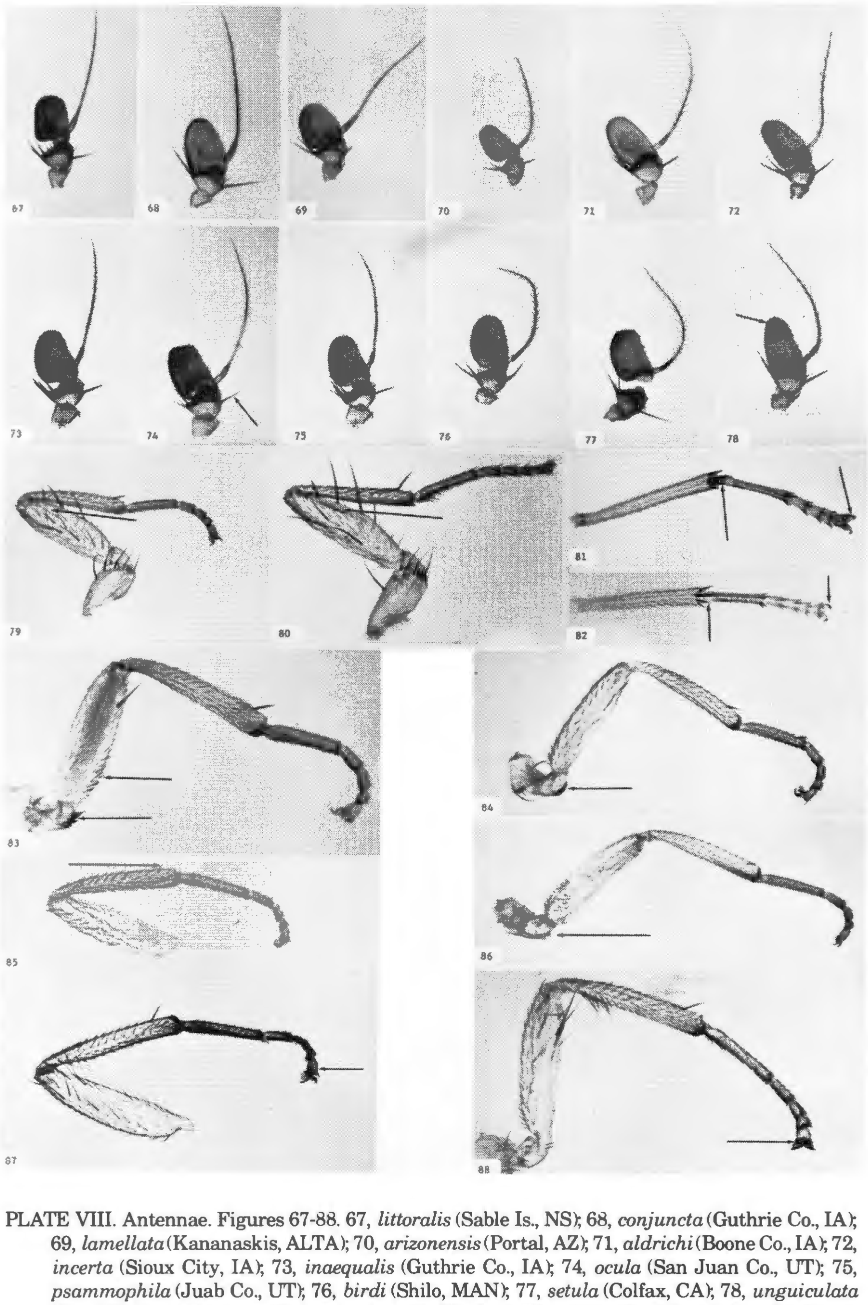

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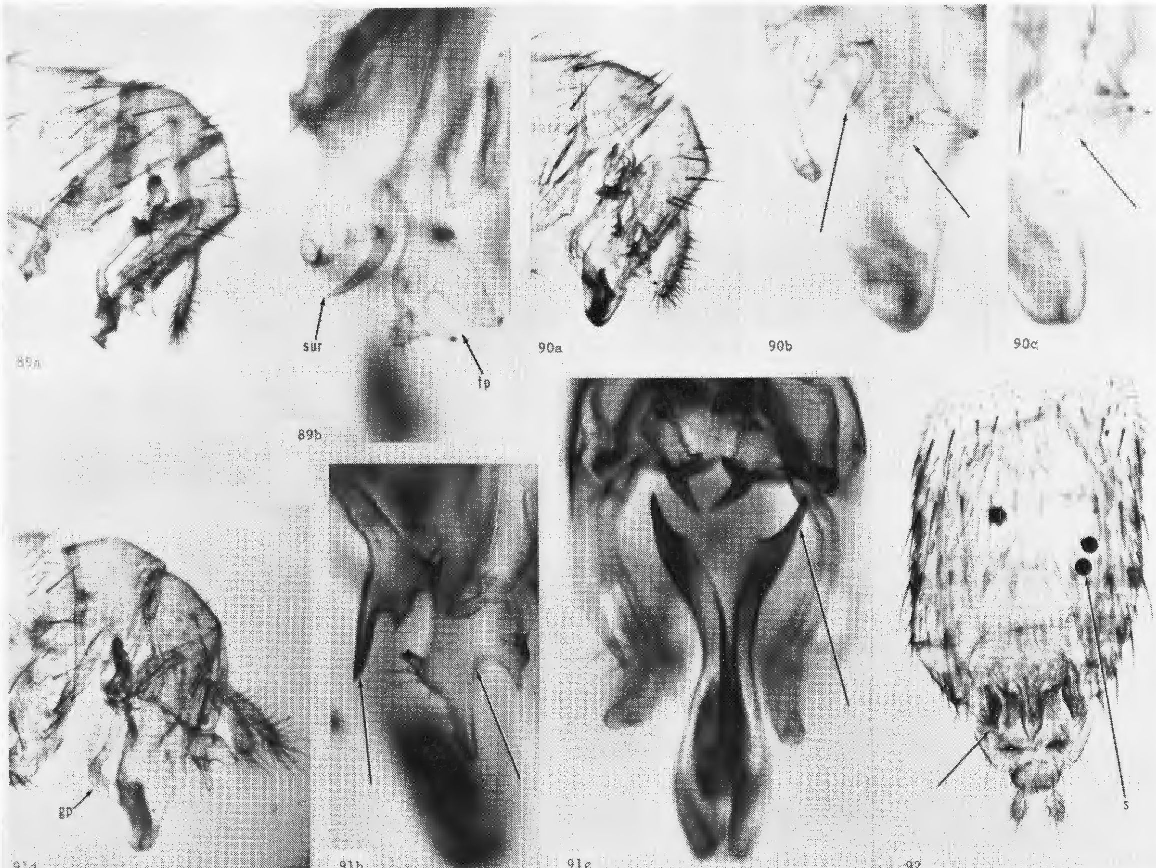

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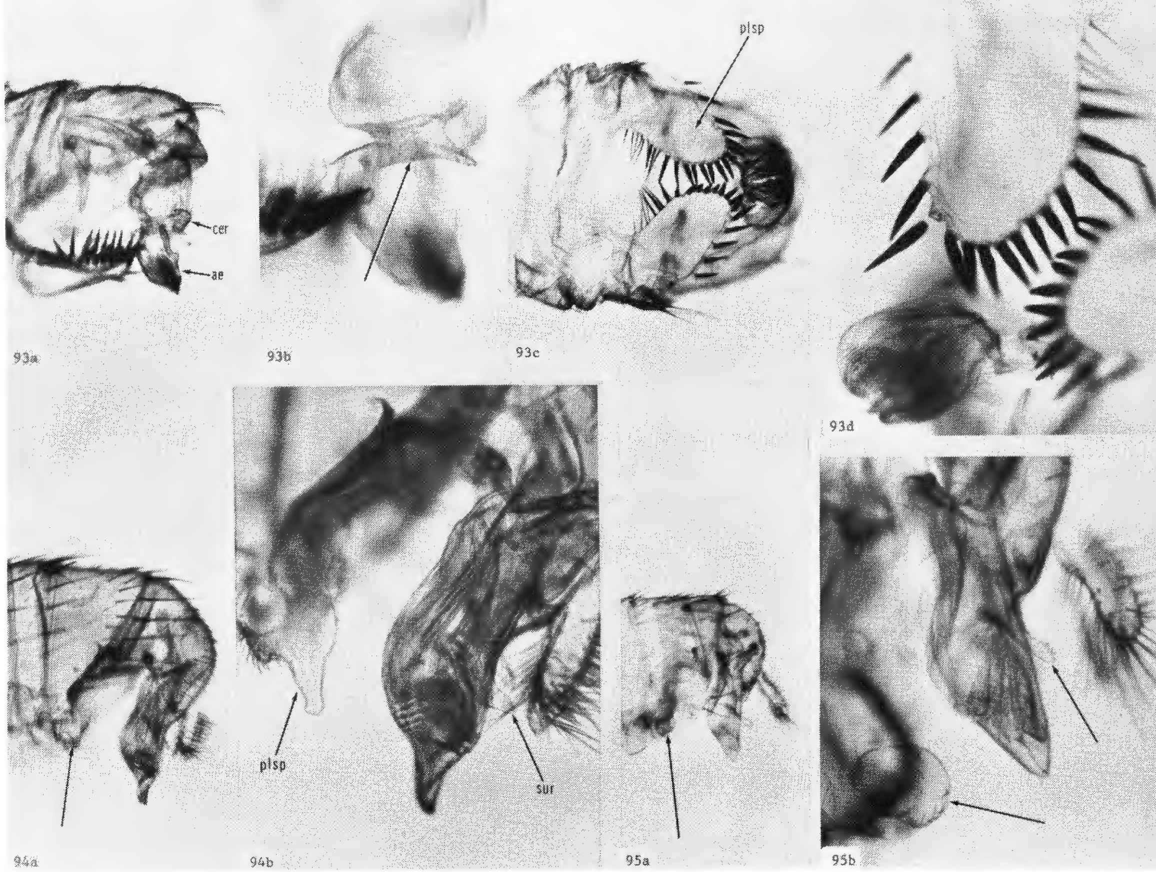

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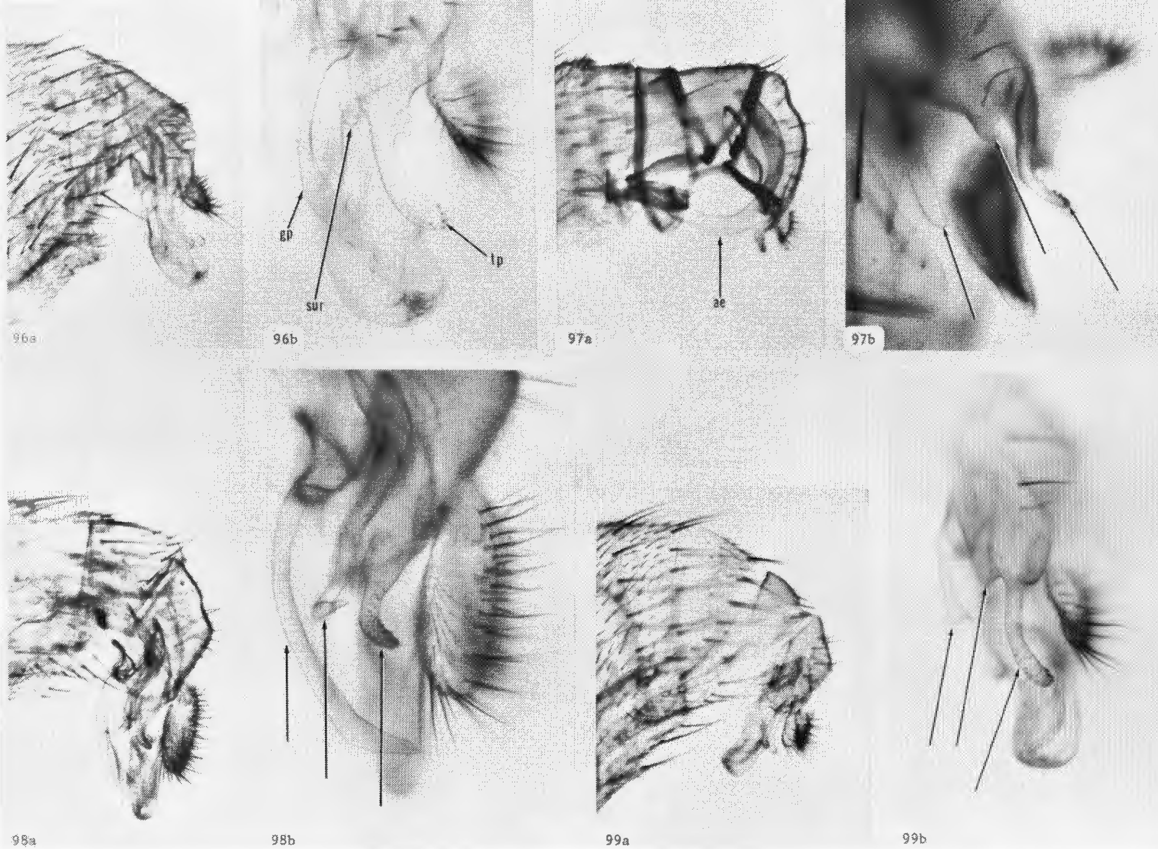

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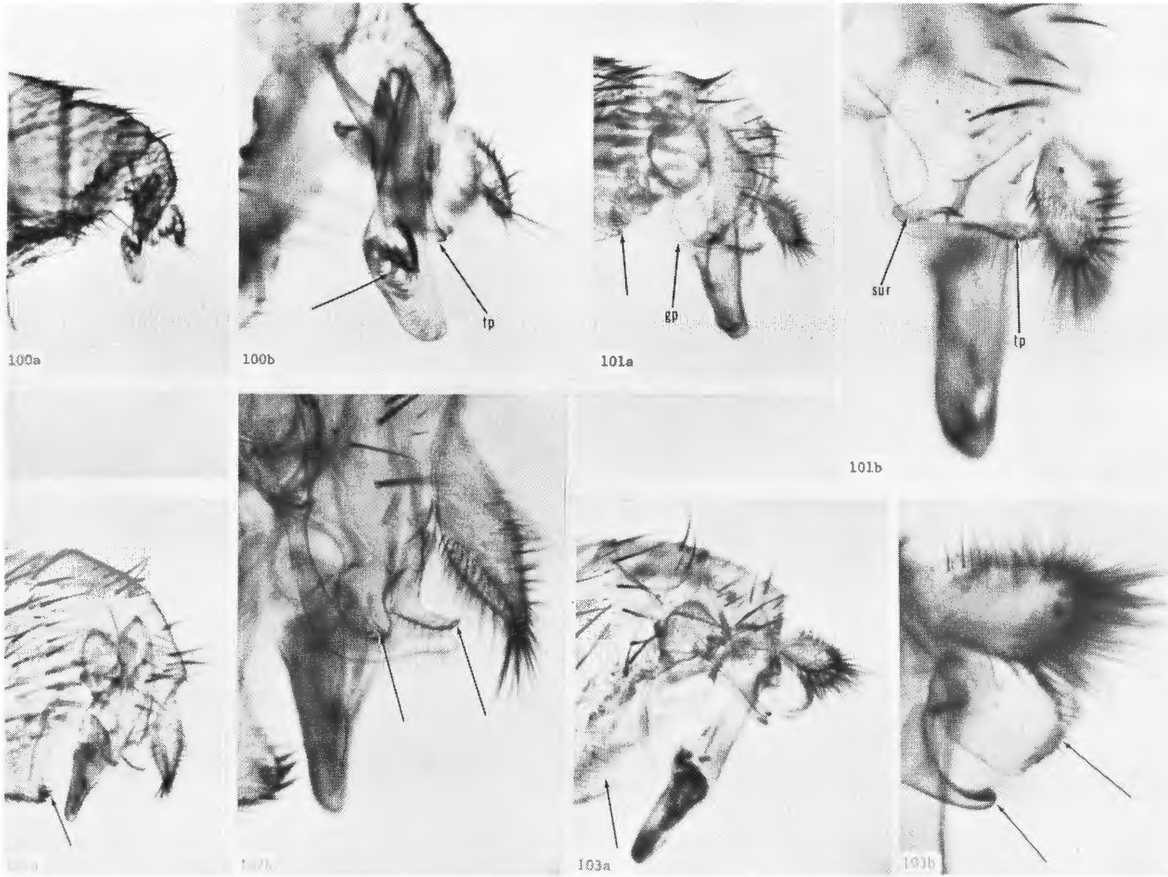

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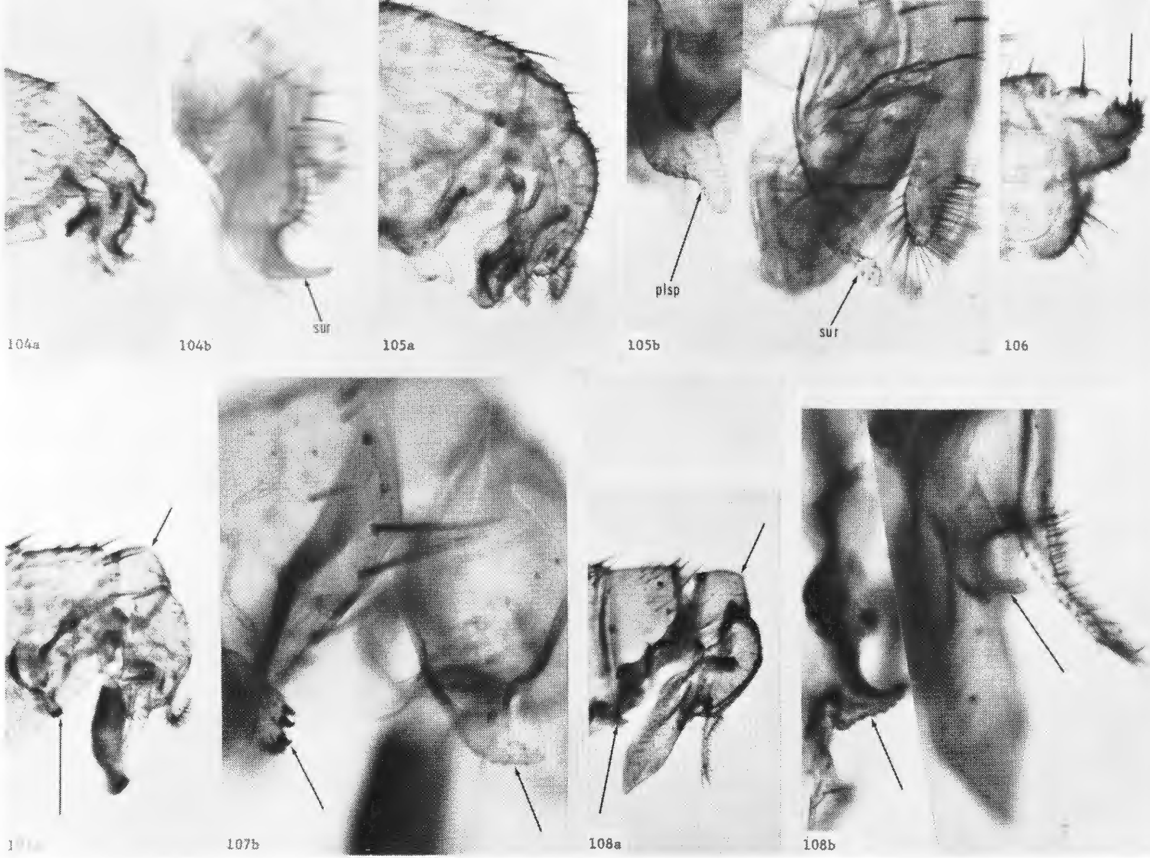

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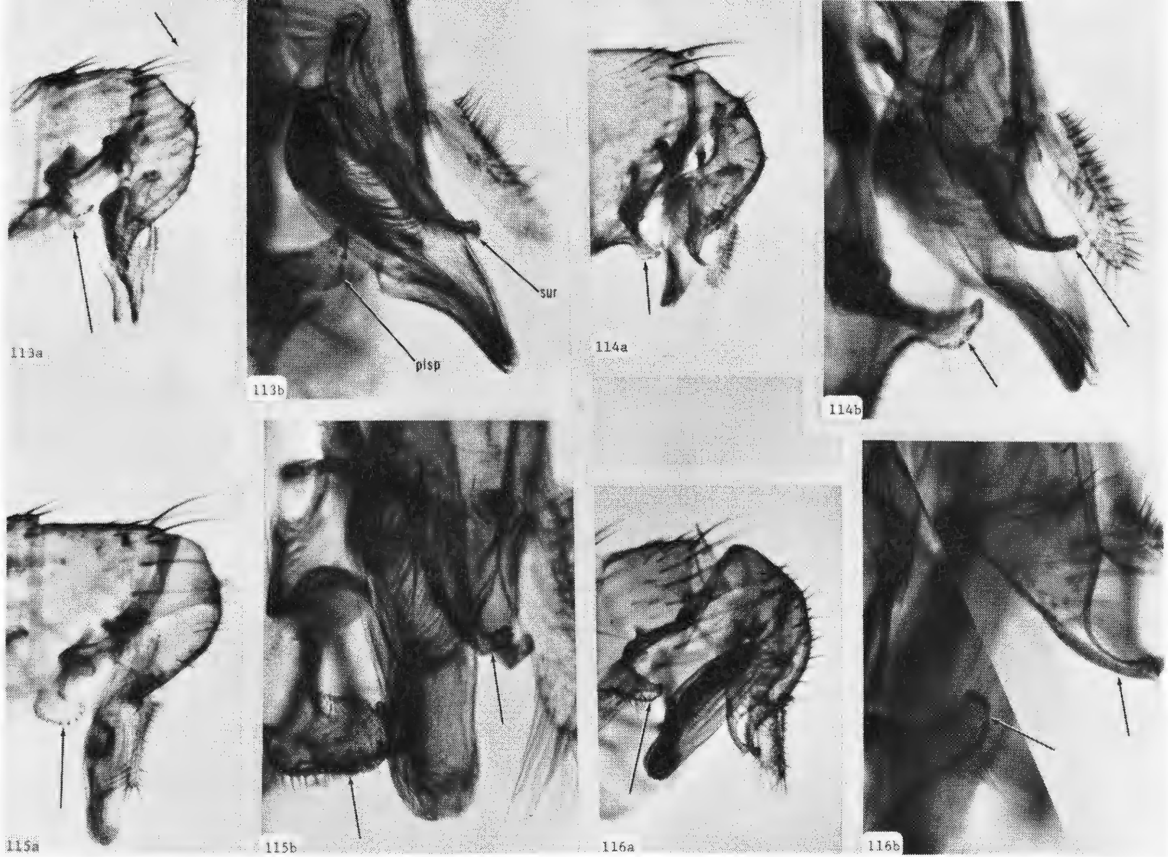

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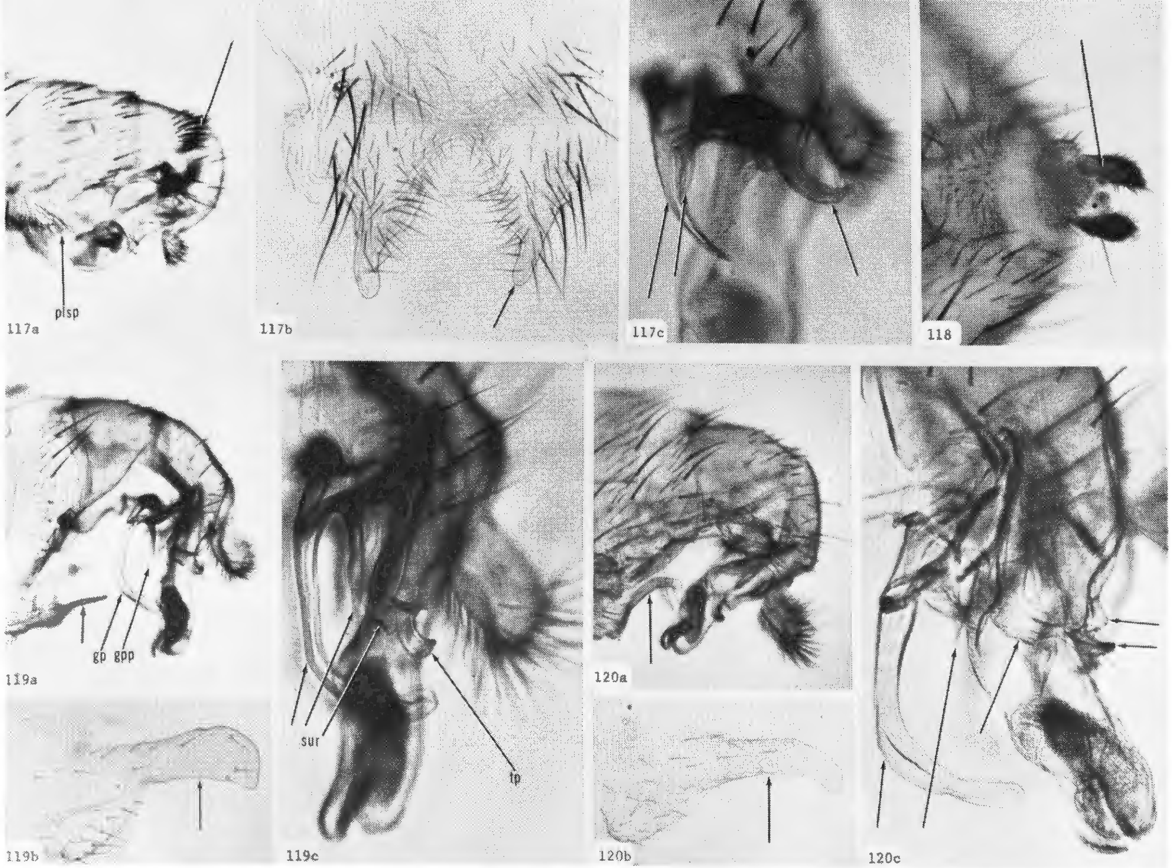

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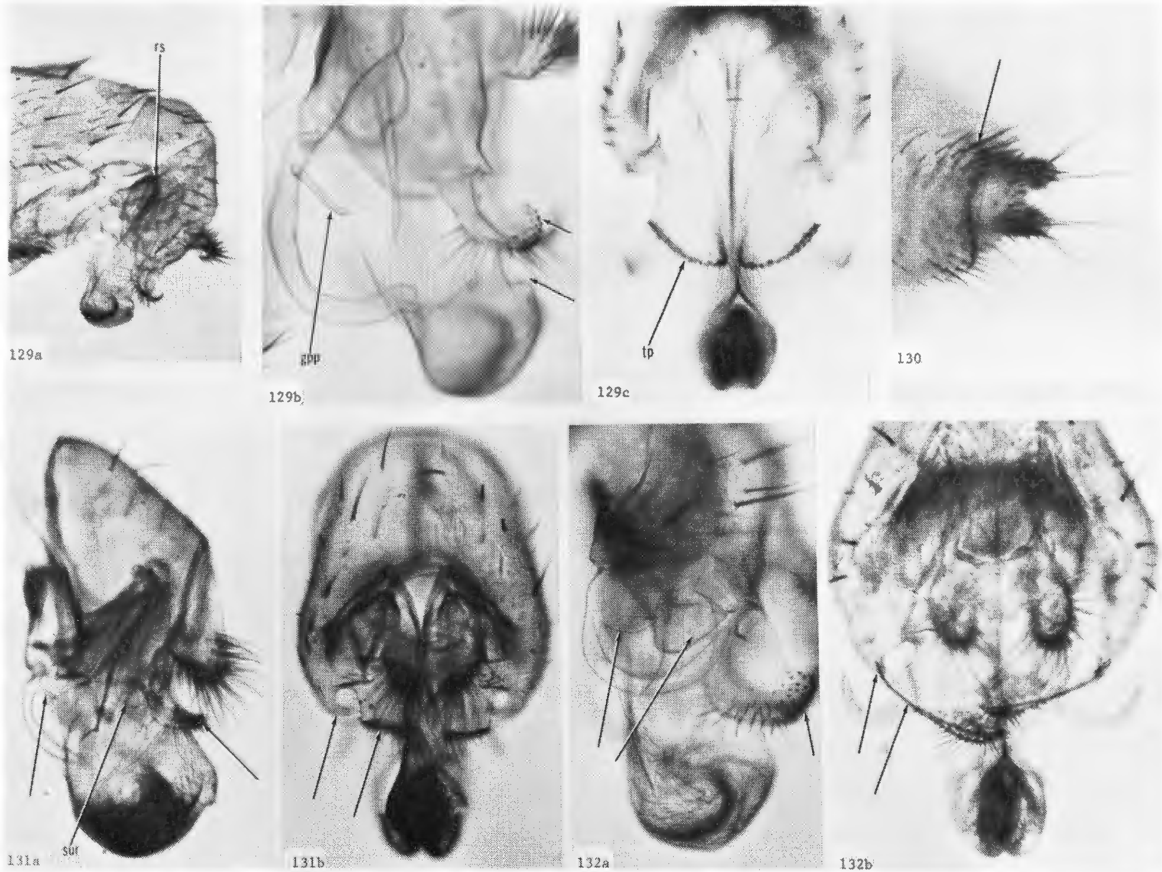

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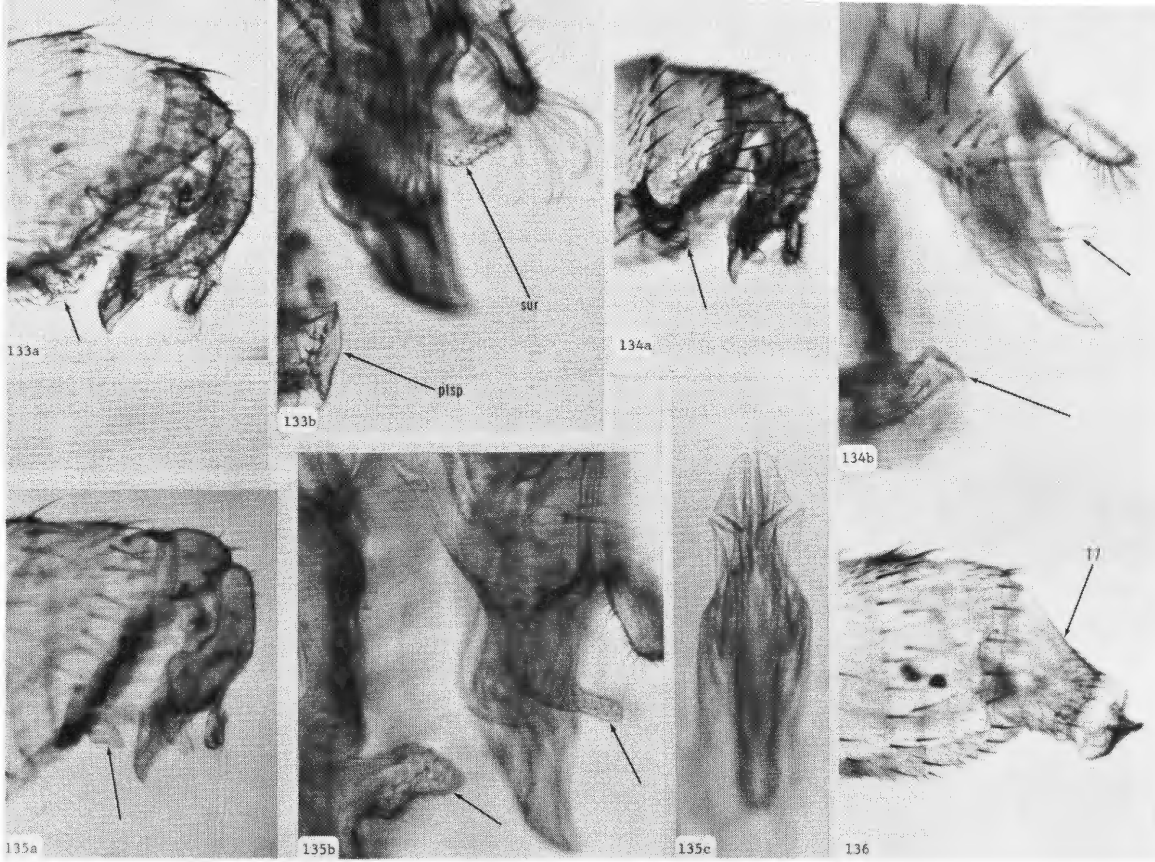

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LOCATION OF NEW INDUSTRIAL FIRMS: ANALYSIS OF SIZE OF TOWN AND FIRM CHARACTERISTICS*

David L. Rogers and Willis J. Goudy†

ABSTRACT. This study reports on firms that located in Iowa communities between 1965 and 1974. Benefits produced by the firms for their host communities and for individual workers employed in these firms are examined. Data were obtained from mail questionnaires returned by 136 firms in the state. Concerning community benefits and the size of town in which firms located, only two of nine tests reached statistical significance; the number of jobs added by firms was greater in larger communities and the proportion of nonproduction workers decreased with size of the host community. Several differences were observed in benefits flowing to employees. Among the nine of the 27 variables statistically related to size of the host community were production days lost, on-the-job training, internal promotion, pension plans, and military and maternity leaves of absence. But in general, firms locating in Iowa's small towns provided essentially the same benefits to communities and employees as those locating in intermediate and large towns.

INTRODUCTION

This report examines the characteristics of firms that located in Iowa communities from 1965 through 1974. Several variables influencing the decisions of new firms to locate in certain towns have been examined in other studies, including distance to raw materials, distance from markets, availability of physical and transportation facilities, utility rates, taxes, and the availability and cost of labor (Helgeson and Zink, 1973; Howard, 1970; Fuchs, 1962; Moses and Williamson, 1967). No studies were located, however, in which the quality of firms locating in communities of different sizes was described. As used in this paper, quality of firms reflects benefits produced by firms for their host communities at large and for the individual workers employed in these firms. Two sets of community benefits will be explored. The first set includes direct benefits: type of firm, jobs added, increased payrolls, and contributions to residents and civic organizations. The second set includes less direct benefits to the community: potential for employee contributions to the community, workforce composition, potential for firm mobility, and location of ownership.

From the perspective of the individual employee, the following items will be examined: employee salaries; safety; management-employee procedures including selection, training, appraisal, and promotion; and company benefit packages. All of these community and employee

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benefits will be examined within the context of the general question: Do the characteristics of new firms differ by the size of Iowa communities these firms selected for location and operation? For purpose of analysis, communities were divided into three categories of population size: 200 to 2,499; 2,500 to 9,999; and more than 10,000.

PROCEDURES

Data were obtained from mail questionnaires sent to representatives of a random sample of firms that began operating in Iowa communities from 1965 through 1974. The sample of manufacturing firms was drawn from a list of firms compiled and published by the Iowa Development Commission. Of the 473 questionnaires mailed to the heads of firms, about one-third (154) were unclaimed at the post office or were marked as being out of business. This left 283 firms assumed to be in operation when the first questionnaire was sent in the spring of 1975. Forty-eight percent of these firms (136) returned their questionnaires after four mailings (original questionnaire, post-card reminder, second questionnaire, partial questionnaire after a telephone contact).

The 10-year time period was arbitrarily divided into three nearly equal categories. Table 1 reveals that the largest percentage of the new firms began operation in the last (1972 to 1974) of three time periods over the decade. Intermediate-sized towns experienced the greatest activity during the 1972 to 1974 period, but locational activities of new firms were distributed fairly equally throughout the entire 10-year period in the smallest and largest towns.

In addition to time of location, respondents listed the products being sold by their firm. These were coded according to Standard Industrial Categories as defined by the U. S. Bureau of the Census. A wide variety of firms located in Iowa during this time period, as shown in Table 1. Smaller towns were the recipients of chemical, food, and machinery firms, whereas intermediate-sized towns tended to receive and retain firms of all types with equal frequency except for those producing miscellaneous nondurable and stone products. Larger communities tended to add and retain machinery and miscellaneous nondurable firms and also fabricated metals. When the industrial categories were reviewed, the food industries were distributed fairly equally among the different-sized communities. Chemicals, however, tended to concentrate in smaller towns; these were primarily agriculturally oriented firms. Metal fabrication and machinery located and remained in larger rather than smaller towns, probably because of the need for more employees than some of the other types of firms.

Table 1. Time of Location and Standard Industrial Classification of Firms by Size of Town

	Size of Town		
	200-2,499	2,500-9,999	10,000+
Time of location:			
1965-1967	36%	23%	36%
1968-1971	26	22	33
1972-1974	38	55	31
Type of firm:[a]			
Non-durable:			
Food	19%	19%	14%
Chemical	31	14	10
Miscellaneous non-durable	7	8	27
Durable:			
Stone	10	8	2
Fabricated metal	10	17	15
Machinery	14	16	27
Miscellaneous durable	9	18	5
Number (Maximum) of Firms	42	51	42

[a] Significant differences greater than the 0.05 level (chi-square) between the size categories.

RESULTS

Community benefits and size of town

Among the major benefits that may be added to a community with the arrival of a firm are new jobs, increased payrolls, financial contributions to local organizations, released time for employee contributions to the community, and firm contributions through scholarships. Jobs are the primary benefit sought by community leaders (Wadsworth, 1966). Numerous case studies report the number of new jobs added with industrial expansion (Summers et al., 1976). The number of these new jobs in communities reported in the literature ranges from about 25 (McElveen, 1970) to 1,900 (Brady, 1974). Because firm location usually is studied in a single community, there is no information about whether larger firms located in larger or in smaller towns, thereby increasing the amount of employment more in one size category than in another.

Respondents indicated the temporary and permanent size of their work force. Table 2 shows the median number of permanent jobs added per firm in towns of different size. The relationship is direct; as the size of town in which a firm located increases, so does the number of jobs added to the town. This relationship also holds when temporary employees are combined with permanent employees. The relationship between median number of jobs per firm and size of host community is statistically significant.

Table 2. Community Benefits by Size of Host Town

	Size of Town		
Benefits to Host Community	**200-2,499**	**2,500-9,999**	**10,000+**
Direct			
Median number of permanent jobs added per firm[a]	5.0	20.5	71.9
Median annual payroll added per firm	$95,892	$176,800	$152,215
Median financial contribution to civic organizations per firm employee	$7	$13	$18
Percentage giving release time to employees for community activities	70%	60%	63%
Percentage giving scholarships to community residents	10%	4%	14%
Indirect			
Median proportion of non-production workers per firm[a]	.50	.18	.25
Median proportion of female workers per firm	.16	.20	.74
Percentage of firms that are:			
locally owned	52%	41%	35%
branch plants	43	49	52
other	5	10	12
Median value of depreciable assets per firm	$186,500	$431,400	$274,000

[a] Significant difference at the 0.05 level by use of the "Extension of the Median test." Median values were used because of the extreme values occurring in some of these variables.

In addition to increases in jobs, community leaders also seek new industry to increase the amount of disposable income available for circulation in the community. Following the positions taken by Thompson (1969) and Hanson (1974) that rural communities are at the lower end of the filtering-down process of firms, thus receiving slow-growth industries paying low wages, we expect that payrolls will be smaller in the more rural communities.

Differences between the median annual payrolls of firms that had located in smaller and larger areas support this expectation in part. Median payrolls are smallest in smaller communities, but the two larger size categories have almost equal median annual payrolls from these firms. Overall, the association between payrolls and community size is not statistically significant.

Three direct contributions made by firms to their host communities (on which no previous studies are available) are monetary, released time, and scholarship. We have no reason to expect differences in contributions of these types between firms locating in large or small communities. The percentage of firms providing release time is relatively high in all towns and does not vary significantly between the different size categories. Also, there is no significant association between town size and the percentage of firms providing scholarship programs or in the median financial contributions to civic organizations.

In addition to direct benefits, four indicators of indirect community benefits are thought to be associated with manufacturing firms. These factors are labeled indirect because of the assumptions made about their operation and because they reflect potential rather than actual events.

We examine the type of employees added in these firms because it suggests something about the potential contribution that could be made by these employees in solving community problems and in improving the quality of life in the host communities. Maitland and Friend (1961), for example, reported that new employees were involved in community activities to the same or a greater extent than were local residents. Summers et al. (1976) found that most of the community leadership associated with new employees came from workers with higher education. With Wadsworth (1966), we argue that new industries contribute brainpower for making communities better places in which to live through the activities of managerial and supervisory personnel who come to live in the town.

We selected the nonproduction workers in these firms to reflect potential contributions that might be made by firm employees. In keeping with the logic of Thompson (1969), we expect that a smaller proportion of nonproduction employees will be found in firms locating in smaller towns, thereby decreasing the potential contribution of firms to this category of communities.

Table 2 shows that firms with larger proportions of nonproduction workers are found in the smaller towns. The median number of nonproduction workers in the smallest towns is largest and the data show a statistically significant association between nonproduction employees and size of the host community. When permanent employees are considered alone, the results are the same as when temporary and permanent workers are grouped together.

The second indirect indicator of community benefit is the male-female composition of the employees added in these firms. We expect that firms locating in smaller towns will have larger percentages of female employees. This expectation is derived from two sources. First, Thompson's (1969) theory suggested that firms locating in small rural towns would be on the lowest rung of the filtering process (low skill, low wage, labor intensive). Second, an examination of 22 case studies reported in Summers et al. (1976) showed that firms locating in larger towns employed, on an average, a smaller percentage of females than did firms locating in smaller towns. In our data, although the proportion of female workers varies widely (Table 2), the differences are not statistically significant. And the average percentage of workers who are female is smallest in the firms locating in smaller towns rather than largest as we expected.

Whether firms are locally or absentee-owned may make a difference for the host community. Absentee-owned firms have been shown to influence community decisions and community leadership structures (French, 1969; Schulze, 1958; Clelland and Form, 1964). We expect that locally owned firms will be more responsive to local needs; therefore, locally owned firms are defined as being more beneficial than absentee-owned firms, other things being equal. The data in Table 2 show a tendency for locally owned firms to gravitate to, and to remain in, smaller towns and for branch plants (absentee-owned) to locate in larger towns; this relationship is not statistically significant, however. The fact that more firms in small towns are locally owned probably contributes to the larger financial contribution and release time programs evidenced by small-town firms.

The last indicator of indirect benefits is captial intensity as measured by the value of depreciable assets. We expect that firms with greater investments in land, machinery, and facilities will be less mobile and, therefore, more likely to be a permanent institution in the community. Thompson (1969) and Hansen (1974) both argue that smaller towns may be receiving firms that are more labor intensive, firms that are looking for competitive advantages associated with labor-intensive operations. We expect, therefore, that more labor-intensive rather than capital-intensive firms will locate and remain in smaller towns. The data in Table 2 reveal that the expected trend does occur; the more capital-intensive firms locate in larger communities. The differences, however, are not large enough to be statistically significant.

Employee benefits and size of host town

The only previous discussion of employee benefits by size of town in which firms locate is Thompson's (1965) argument that firms in small rural towns tend to pay lower wages. Therefore, we expect that firms with lower wage levels will locate in smaller towns. The data in Table 3 support the proposed direction of this relationship; firms reporting from larger communities tend to pay higher wages than do those in small towns. But the differences for exempt employees (management) and for nonexempt employees (production, clerical, and secretarial staff) are not significant between size-of-town categories.

Although the number of lost-time injuries does not differ by size of town, the number of production days lost from injuries is significantly higher in firms in larger towns. The tendency is for firms in larger communities to report more lost-time injuries and more production days lost.

Other factors affecting employees include procedures used by management to select, train, appraise, and promote personnel. Data in Table 3 indicate that methods of selecting personnel are not associated with the size of town in which the firms locate. There is, however, a slight trend in the direction of greater use of paper-and-pencil performance tests in the firms in larger towns. Of the training procedures, only the percentage of firms offering on-the-job training increases significantly with the size of host town. The more formal techniques of appraisal vary with the size of town. Scheduled verbal and written procedures are more frequently used in firms located in larger communities. The unscheduled procedures, however, do not vary to a statistically significant degree. Finally, internal promotion to management positions is higher in firms locating in larger towns.

Four of the fringe benefits frequently offered to employees differ by size of host community. In all instances where there is a statistical association between benefit and size of town, firms locating in the largest communities offer more benefits than those locating in smaller towns. The benefits associated with size of town are pension plans, maternity and military leaves of absence, and education aid.

Table 3. Employee Benefits by Size of Town

	Size of Town		
Employee Benefits	**200-2,499**	**2,500-9,999**	**10,000+**
Mean pay per exempt employee per firm	$11,754	$14,178	$15,861
Mean pay per nonexempt employee per firm	$5,290	$5,620	$6,100
Mean number of lost-time injuries per employee per year per firm	0.04	0.12	0.23
Mean number of production days lost per employee per year per firm	0.16	1.57	0.56[a]

Continued on next page

Table 3. (Continued)

	Size of Town		
Employee Benefits	**200-2,499**	**2,500-9,999**	**10,000+**
Selection methods:			
% using face-to-face selection	95%	100%	100%
% using paper-and-pencil performance tests	19%	24%	32%
Training methods:			
% using on-the-job-training	73%[b]	94%	93%
% using classroom instruction	29%	25%	33%
Appraisal methods:			
% using unscheduled verbal appraisal	73%	68%	82%
% using scheduled verbal appraisal	35%[b]	52%	65%
% using unscheduled written appraisal	16%	23%	39%
% using scheduled written appraisal	37%	43%	67%[c]
Mean number of management employees promoted from production and clerical groups within firm	2[d]	6	9
General Benefits:			
% having a pension plan	44%	41%	74%[c]
% having paid vacations	91%	96%	100%
% having paid holidays	88%	98%	100%
% having group health insurance	86%	90%	98%
% having group life insurance	76%	86%	95%
% having a credit union	18%	20%	36%
% having maternity leave of absence	48%	47%	82%
% having military leave of absence	59%	57%	82%[c]
% having education aid	39%	47%	72%[c]
% having supplemental unemployment plan	20%	18%	20%
% having severance pay	48%	38%	43%
% having extended vacations	18%	10%	15%
% having stock options	28%	18%	15%
% having a thrift plan	13%	14%	16%

[a] Significant differences greater than the 0.05 level (t-test).
[b] Significant differences between this category and both larger ones (chi-square, 0.05 level).
[c] Significant differences between this category and both smaller ones (chi-square, 0.05 level).
[d] Significant difference between this category and the largest one (t-test, 0.05 level).

CONCLUSIONS

Competition for new firms is such that some authors suggest that the smallest rural communities, although happy to get them, often receive the so called "leftovers" in terms of firms locating within their boundaries. Supposedly, these firms are less likely to benefit the community than those locating in larger towns. When direct community benefits generated by firms that have located in the town over the last 10 years are examined in this study, however, the only statistically significant difference between three community-size classes is the number of jobs added. For indirect community benefits, or those potentially assisting a community, only the median number of nonproduction workers (management) is associated with size of host community, but this is contrary to what was hypothesized. Thus, benefits accruing to a community from the location of a firm do not vary by size of community to the extent suggested by authors of single-community studies. Greater differences are observed on employee benefits from new firms when the communities in which these firms located are grouped by size. Nine of the 27 variables differ significantly; in eight instances, a larger proportion of firms in the larger communities provides the employee benefits than do those firms in the smallest size class. Only on the number of production days lost is it evident that employees of firms in the smallest towns benefit to a statistically significant degree more than do those in the largest towns.

Firms operating in large communities tended to report the highest levels on the variables where relationships occurred whether that was a positive (internal promotion) or a negative (injury rate) evaluation of the impact of the firm on the local community. For those variables for which statistical significance was not reached, relationships also tended to be direct; again the firms locating in the largest communities usually reported the highest levels on these characteristics. Thus, the quality of benefits to individual employees and to the community from the new firms were both positive and negative; whereas the larger communities gained greater rewards for attracting new manufacturing industries, they also reaped greater costs on some factors.

These findings indicate that our indirect test of the "trickle down" theory of firm location was not upheld, at least in the relationship between firm benefits to communities and employees and community-size classifications. But this conclusion must be tempered with the realization that we've studied only those firms locating and continuing to operate in Iowa communities from 1965 through 1974. Examination of firms going out of business was not attempted, and it could be that disproportionate numbers of firms with excellent community and employee benefits were lost in one size of community over that same time period. Also, some communities may have realized the location or development of firms particularly noted for providing local benefits before the initial point of this study. Thus, they might have no need for attracting additional firms. What we can conclude is that the impacts on community and employee benefits of those firms that arrived sometime between 1965 and 1974 and survived until 1975 did not vary greatly in terms of community size classifications. In general, those firms locating in small towns provided essentially the same benefits as those locating in intermediate and large communities in Iowa.

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THE DEVELOPMENT OF SHAW'S TEACHER-HERO

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No reader of Shaw's plays can fail to detect their didacticism, since Shaw rarely contents himself with offering the play itself, but often adds pointed and convincing prefaces to clarify his arguments. As Robert Brustein puts it, the reader of a Shaw play experiences not only the play, but "a hailstorm of prefaces, postscripts, disquisitions, chatty stage directions, and other prose addenda,"[1] all of which are Shaw's devices to guide the reader to a clearer perception of the fundamental issues presented in the play itself. But these elements of didacticism, which arise out of Shaw's authorial intrusions in the text, are not the deepest thread of didacticism in the dramas. The audience of a play, who must experience it without the benefit of Shaw's prefaces and addenda, also feels the didactic purpose working through the characters themselves. Shaw does not rely entirely on his prose prefaces to make sure his point is made, but in his greatest plays, he builds a didactic, pedagogic tendency into the major characters he creates. Whatever else they are, Ceasar, Undershaft, and Shotover, the respective heroes of three very different plays of Shaw, are teachers. They are teachers not only in the sense that Shaw uses them as a tool for expressing ideas to his audience, but more importantly, they are engaged in teaching important lessons to other characters of the drama. More specifically, they concentrate their efforts, in each case, on teaching a particular young woman, around whose education Shaw's drama is built.[2] The pattern of the older male as the teacher of the younger female is consistent in *Caesar and Cleopatra* (1898), *Major Barbara* (1904), and *Heartbreak House* (1916), plays which must be acknowledged as among Shaw's finest.[3] Even though he pursues different themes through different characters and settings in these plays, Shaw consistently uses the structural principle of didacticism in the plays. By focusing on this teacher-student relationship in these plays, particularly as it relates to the image of the teacher as hero, we can observe Shaw's changing attitude toward the nature and process of teaching itself. Curiously, such a focus on the nature of the teaching process culminates in an expression of faith in teaching in *Heartbreak House*, a play that in many other respects reveals a somewhat disillusioned Shaw. That expression of faith is intelligible only in the context of the earlier plays, *Caesar and Cleopatra* and *Major Barbara*, which depict the process of teaching in quite different terms. Shaw's changing conception of the didacticism that is a basic structural element in all of these plays in the subject of this essay.

In the earliest of these plays, *Caesar and Cleopatra*, Shaw's model of a political leader, Caesar, is introduced almost immediately as a teacher. After an initial confrontation, Caesar attempts to calm Cleopatra's fears by asking her, "Shall I teach you a way to prevent Caesar from eating you?" Cleopatra desperately responds, "Oh, do, do, do" (2,186), thus placing herself in the role of Caesar's pupil, a role which she maintains throughout the play. This assumption of the roles of teacher and pupil is not wholly unprepared for, however, when one notes Shaw's strategy of associating Cleopatra with the small "white cat" and the "little kitten of a Sphinx" (2,185), while he

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associates Caesar with what Caesar thought was the true Sphinx—"Have I read your riddle, Sphinx?" (2,182)—and has Cleopatra say that "His father was a tiger" (2,185). The relationship of great to small, of mystery and power to childish imitations of power, is from the beginning the basis of Caesar's relation to Cleopatra.

Yet, what is most striking about Shaw's portrayal of Caesar is his consistent attempt to deflate his hero at the same time he demonstrates his heroism. In the opening scene of Act I, when Caesar addresses the Sphinx, we are alerted to the fact that Caesar is above the ordinary mortal.

> In the little world yonder, Sphinx, my place is as high as yours in this great desert; only I wander and you sit still; I conquer and you endure. . .Sphinx, you and I, strangers to the race of men, are no strangers to one another. (2,182)

But when the girlish voice of Cleopatra scares him, and we later find the Sphinx he addressed was only her "pet Sphinx," Caesar seems comically mortal. This blending of the heroic and the comic in Caesar's character is most forcefully apparent when in Act II, after his political and military maneuvering successfully diverts the Egyptians' attention to saving their library, Cleopatra comes into his chamber and discovers that he is bald (2,221-222). Shaw's purpose in such a mixed portrayal of Caesar is, on one level, to make a great man human and understandable. The constant reminders of Caesar's age, the glimpses of his weaknesses and lapses, and his own wry and self-deprecating humor keep that humanity constantly before us.

Because he is a believably human character, Caesar is also a potentially effective teacher. Shaw demonstrates that it is not a kind of superhuman intelligence or ability that makes a great political leader, but rather a consistent application of reasonable principles to politics. If greatness is the exercise of reason, it is available to anyone willing to live reasonably. Caesar's political astuteness, therefore, can be taught, and Caesar is always more than ready to teach it, as he shows in his relation with Cleopatra. The dramatic tension of the play centers on his attempts to teach the art of government, principally to Cleopatra, who seems to need the lessons the most, and also to his own followers and enemies. These attempts to teach, however, are not isolated pedagogical interludes in the play. They are rather the action of the play itself. Caesar teaches by doing, and thus the story of his actions as a conqueror in Egypt is also one extended lesson in the application of reason to politics.

Even in the first lesson he gives Cleopatra, that she should rule her servants and not vice-versa, he proceeds not by lengthy explanation but rather by reducing Ftatateeta to cowering submission:

> On your knees woman: am I also a child that you dare trifle with me? [*He points to the floor at Cleopatra's feet. Ftatateeta, half cowed, half savage, hesitates. . .Caesar takes his sword by the scabbard. . .*] Have you remembered yourself, mistress?
>
> *Ftatateeta, crushed, kneels before Cleopatra.* (2,190)

Caesar's exemplary actions, however, are not generally of the sort which require great displays of strength. Instead, they require compassion, common sense, and the ability to judge the people he encounters. Thus to Cleopatra's amazement, he refuses to execute his Egyptian enemies Pothinus and Achillas in Act II, or his reluctant servant Rufio in Act III, after showing her in the scene above, that the threat of death can be a useful tool for a ruler. Always conscious of his double role as ruler and teacher, he encourages Cleopatra at the end of Act II, to "Go to the balcony; and you shall see us take the Pharos. You must learn to look on battles" (2,223). That Caesar remembers his responsibility to teach Cleopatra at this crucial point emphasizes his conscious desire to serve as a teacher.

The problem inherent in Caesar's double role is that although he succeeds as a politician, he fails as a teacher. Cleopatra's order that Ftatateeta kill Pothinus in Act IV, a step that Caesar has twice refused to take in her presence, is the final evidence of his failure, and Shaw's final condemnation of the world and its unenlightened politics. Charles Berst, in commenting on the failure, lays the blame for the failure on society, of which Cleopatra is the creation:

> Cleopatra can only be superficially educated because instinctively she is a creature of her cultural heritage, and Shaw emphasizes that instincts, rather than reason, control man's behavior.[4]

While there can be no doubt that the deep running social conditioning which stands in the way of reason is much to blame for Caesar's failure to teach, it should be said that part of the blame is Caesar's as well. Caesar is, as critics have noted, an isolated hero.[5] His indifference is a constant source of irritation for Cleopatra, and an occasion for Shaw's humorous portrayal of her vanity, but it is also a problem for Caesar himself, who knows that a conqueror must deny his emotions. There is inner tension between Caesar's pragmatism and his emotions, a tension we see only when he lapses (or ascends) into his rare poetic effusions. The first glimpse we see of him is as a lonely wanderer, telling the Sphinx of his "exile" in the world, and his inner hunger. In Act II, when he hears of the death of Lucius Septimus, he delivers a moving speech of regret not only for that death, but for the murders forced upon him by politics in the past. But, most convincingly, just before the death of Pothinus in Act IV, Caesar seems to be putting politics behind him in his plan to make his relationship with Cleopatra a much deeper one:

> Cleopatra, will you come with me and track the flood to its cradle in the heart of the regions of mystery? Shall we leave Rome behind us—(2,270)

Caesar's growing eagerness to "leave Rome behind" is the dramatic evidence of his realization of what a difficult lesson he is attempting to teach. The goal of his teaching is purely political, and though the final accomplishment of his political goals would be a fairer society, Caesar cannot, or will not, teach the personal qualities necessary to enable Cleopatra to carry out his politics. In order to be a successful ruler, Caesar must be impersonal and isolated, but in order to be a successful teacher, he must somehow overcome the barriers between him and those who would learn from him. His retreat from a close relationship with Cleopatra, as evidenced in his forgetting her in the final act, saved him as a ruler, but doomed him as a teacher and ultimately as a complete human.

For Caesar, the creation of a just ruler and thus an ideal society is the end of teaching, but for Andrew Undershaft, in the later *Major Barbara* (1904), the creation of an ideal society is the means to his teaching. Undershaft's credibility to Barbara is established through his utopian industrial village. Only by demonstrating the superiority of eradicating poverty, rather than trying to teach men to ignore it, can Undershaft gain the respect and attention of his strong-willed daughter. But Undershaft's village is a means to teaching in a much larger sense as well: in it, he has created what he feels is the only environment in which Barbara's kind of teaching, spiritual teaching, can be accomplished. This ultimate goal of spiritual teaching, or salvation, makes *Major Barbara* radically different from *Caesar and Cleopatra*, which has politics as its ultimate goal.

Undershaft, unlike Caesar, must prove himself to Barbara, and to the audience, because of his questionable moral position as director of a munitions factory. Stephen Undershaft's story, early in Act I, about the "little Brute at King's" who inscribed his Bible with the phrase "Son and heir to Undershaft and Lazarus, Death and Destruction Dealers" (3,72) prepares us for the moral censure that society, which has made Undershaft rich, also heaps upon him. Undershaft's defense of his moral position, however, is to be aggressively undefensive. Not only is he "unashamed," as his motto proclaims, he is a conscious proselyter for his morally questionable manner of living and view of society. It is his desire to teach and convert that is the basis of his interest in Barbara's involvement with the Salvation Army. As he tells Lomax in Act I,

> One moment, Mr. Lomax. I am rather interested in the Salvation Army. Its motto might be my own: Blood and Fire. (3,88)

Undershaft's eagerness to engage Barbara's thinking about religion sharply contrasts his apparent unconcern about the rest of his family—he could not even recognize his children—and immediately alerts the audience to the fact that he is much more complicated than the expected captain of industry. Like her father, Barbara is also a teacher and converter, and she, not Undershaft, actually initiates the exchange of lessons between the two of them. She says to Undershaft,

> Come down tomorrow to my shelter—the West Ham shelter—and see what we're doing ...Come and see the shelter and then march with us: it will do you a lot of good. (3,88)

Barbara's many resemblances to Undershaft—her disregard for convention, her desire to teach and convert others, and what can only be called her "vitality"—establish a different kind of teacher-pupil relationship in the play. The most important similarity between Barbara and her father, the shared concern about "salvation," emphasizes the fact that both characters have ultimate goals that are similar. The debate of the play centers around the means of achieving "salvation." Undershaft's religious concern is made clear not only through his display of interest in the Salvation Army, but in a pointed remark to his wife: "I do not find it [religion] an unpleasant subject, my dear. It is the only one that capable people really care for" (3,91). Similarly, Barbara's enthusiasm for the Salvation Army leaves no doubt about her religious concern. Thus Undershaft, the teacher, and Barbara, the pupil, are not the radically different characters that Caesar and Cleopatra are. Out of these shared goals and similar personalities, the story of Undershaft's success as a teacher is drawn.

Undershaft, like Caesar, must teach by doing, and his lesson comes in two stages. First he must destroy Barbara's ideal of salvation—the Salvation Army—by confronting her with the reality of the organization's dependence on money. Barbara herself knows the importance of money. In Act II, we see her come from what she calls "a splendid experience meeting at the other gate in Cripps's lane" to ask Jenny, almost immediately, "How much" collection was taken. When she is told "four and ten pence," she responds "if you had only given your poor mother just one more kick, we should have got the whole five shillings" (3,123). Barbara's mistake is to label some money good and some money bad. She tells her father that "two million millions would not be enough. There is bad blood on your hands" (3,124), a conviction that Undershaft destroys with his gift to the Salvation Army. After destroying Barbara's false ideals, Undershaft must, in the second part of his lesson, give her a new vision of salvation. He does this by contrasting the well-being of his workers, who benefit from his bad money, with the wretchedness of her Salvation Army converts. Undershaft's point is that money is a tool, that it cannot be divided into good and bad. Barbara's aptness as a pupil is reflected in her decision to use Undershaft's utopia as a laboratory for her salvationism. She, like Cusins, has realized that all money is tainted by society, but that it can be put to good use. Shaw emphasizes this theme in the preface:

> It is only when it [money] is cheapened to worthlessness for some, and made impossibly dear to others, that it becomes a curse. In short, it is a curse only in such foolish social conditions that life itself is a curse.(3,30)

The implication of such a view of money and society is that social conditions must be corrected before the really important business of salvation can be tended to. Barbara is willing to accept Undershaft's means of social and political reform only because she sees in them the potential of helping her achieve the larger goal of salvation. In a powerful speech at the end of the play she tells Cusins she knew she must "have" the munitions factory because of "all the human souls to be saved" (3,183). Undershaft's politics, his creation of an ideal society, are therefore quite different from Caesar's. Whereas Caesar sees his role as a just ruler and creator of a just society as an end in itself, Undershaft sees his creation of a utopia as the means to personal salvation for his workers. Undershaft's teaching of Barbara, therefore, is the first stage of a much larger pedagogical plan: the disseminating of religious teaching and thus spiritual power, which, as Cusins realizes, is "all power" (3,181).

The play ends on a comically ironic, yet basically hopeful note. The irony lies in the rhetorical triumph of Mephistopheles-Dionysus-Undershaft, and the hope in Barbara's firm determination that salvation will be carried to the munitions workers. Yet the reader who has become sufficiently engaged in the deep moral questions which the play raises about the relationship of man to his immoral society can laugh only tentatively at the play's conclusion. For although Undershaft is certainly persuasive in his analysis of the social changes necessary for personal change, neither he nor Barbara addresses the question of how personal change, or in religious terms, salvation, can be achieved. Undershaft's ideal society is a necessary, but not sufficient condition for salvation. What is even more disturbing is that Shaw, in the preface to the play, gives us every reason to believe that Barbara's attempts to convert the men will fail miserably, because workers attain their dignity from monetary comfort and from little else. As Shaw puts it,

> They [the poor] do not want the simple life, nor the esthetic life; on the contrary, they want very much to wallow in all the costly vulgarities from which the elect souls among the rich turn away with loathing. (3,29)

Shaw, of course, goes on to hold out hope that "it is by surfeit and not by abstinence that they will be cured of their hankering after unwholesome sweets" (3,29), hope that seems tenuous at best for a man who "does not want to live the life of a man of genius" but would rather "live the life of a pet collie if that were the only alternative" (3,30). Shaw's brilliant characterization of the foolishly respectable Cholly Lomax, the priggish Stephen Undershaft, and even the narrowly proper and materialistic Lady Britomart are his own testament to the fact that money is no sure salvation.

The point of this objection to *Major Barbara* is not to denigrate Shaw's brilliant analysis of the problem of poverty and the human indignity it creates. It is rather to indicate where Undershaft's skill as a teacher breaks down. If Undershaft has a method of individual reform as effective as his method of social reform, he never shows it to us. Though he does expose the flaws of Barbara's method of conversion, and provides a new context for her further attempts at proselyting, he does not give her a new method for that conversion—one she certainly needs if she was effective previously only because her "converts were bribed with bread" (3,184). If Undershaft does not have a new method of teaching spiritual power, then he is indeed a "Mephistopheles." He will have seduced Barbara and Cusins into a life of overseeing death, of serving the worst interests of capitalist excesses, without the assurance that a new form of salvation can redeem them. We are left only with the hope in "the will" (3,169) of which Undershaft is a part, a will which gives us as much basis for despair as for hope in the context of the play.

The failure of both Caesar and Undershaft as teachers, although they are very different teachers, can be traced to their failure to teach individual, personal lessons in addition to their political lessons. Both have a vision of society, but Caesar cannot impart the necessary skills to bring it about, while Undershaft cannot impart the individual salvation that would make it worthwhile. Both teachers fail to integrate their reformist political vision with a corresponding vision of individual development. This separation of the social and political realm is precisely the problem Shaw addresses in the preface to *Heartbreak House* when he writes of modern society:

> power and culture were in separate compartments. The barbarians were not only literally in the saddle, but on the front bench in the House of Commons, with nobody to correct their incredible ignorance of modern thought and political science but upstarts from the counting house. (5,15)

Power, as Shaw uses it here, refers primarily to politics. Culture is the category of personal development including art, religion, and learning—all the factors that enhance men as individuals. Shaw laid the blame for the debacle of the war primarily on this separation of politics and culture. If, as some critics feel, Shaw poured more of himself into *Heartbreak House* than into many of his other plays, the reason must in part be his feeling, conscious or subconscious, that even his most powerful teacher-heroes seemed unable to bridge this gap. *Heartbreak House*, recognized as a clear break both in technique and thought from Shaw's earlier drama,[6] is Shaw's most sustained effort to deal with this problem of politics and culture. In the problems it addresses, though not in the conclusions it reaches, it is certainly not discontinuous with the earlier plays.

Shaw handles the problem of the separation of the political and individual realms through the technique of allegory. Shotover's house has the actual shape of a ship, and is allegorically a ship of state. From one point of view, each of the characters can be seen as allegorical representatives of certain classes of English society,[7] although, as Eric Bentley notes, "the things his characters stand for, the points they illustrate, are only a part of their being."[8] As a technique for the unification of power and culture, Shaw's allegory is brilliantly conceived in that the individual choices the occupants of Heartbreak House make gain a political significance when the house is seen as a metaphor for England itself. As we are led through the maze of complicated personal dependencies and relationships of the house, the fact emerges that society itself is an inescapable system of dependencies. Shaw prepares the reader for this allegory in his lengthy discussion of Heartbreak House and Horseback Hall in the preface, which begins with the direct statement that

> Heartbreak House is not merely the name of the play which follows this preface. It is cultured, leisured Europe before the war. (5,12)

But even though the play is allegorical in its inception, or at least supports allegorical reading, it far exceeds allegory and almost any other type of generic categorization. The political allegory gives Shaw a unity of effect, especially when it is read in light of the historical background of the war, but the Chekhovian form gives the play a kind of organic freedom unusual in Shaw's dramatic works. Each of the major characters has a quite different problem to solve, and because Shaw plays nearly every character against every other character, the play is a rapidly flowing presentation of myriad personal confessions, confrontations, and crises. All of these crises flow into the larger political crisis—the threat of war—which ends the play.

There is, however, one relationship in the play that overshadows all the others. What Ellie learns from Captain Shotover is the heart of the play, and only in evaluating this admittedly puzzling relationship can we come to judge the success or failure of Shaw's artistic synthesis of power and culture. Ellie certainly learns in the play—her life does two complete reversals in the course of it. And Shotover is certainly instrumental in her education. But from the outset, Shaw lets us know that this is no ordinary teacher-pupil relationship. The first act begins in the full stride of confusion, Ellie finding herself an unexpected guest in the home of a stranger, who seems annoyed that her suitcase is on the steps. After Shotover mistakes her father for another man in his past, he asks her irrelevantly, but significantly, "Has he attained the seventh degree of concentration?" Ellie then replies with the appropriate ignorance of a prospective student: "I don't understand." Yet Shotover fails to pick up his cue, to fall into the role of the teacher. "But how could he," he replies, "with a daughter?" (5,63). Ellie completely drops out of the dialogue here, and is not pulled in again until Shotover throws away the tea for which she is waiting, promising her "some of my tea" (5,64). Shotover appears at the first to be the essence of senility: unresponsive when he is questioned, yet solicitous of his guest, alternately oblivious and overly sensitive to her. Shaw's portrayal of the teacher and student has undergone a significant change since *Major Barbara.*

The opening encounter between Ellie and Captain Shotover is not out of keeping with their relationship throughout the earlier part of the play, for that relationship is almost nonexistent. Shotover has expressed an unusual kindness in offering Ellie his own tea so soon, as we later find out, but aside from that, he has little to do with her. He seems intent on convincing Mangan that he should not marry Ellie, but his motives seem directed more at saving Mangan from folly than saving Ellie from a bad marriage. The fact that Ellie and Shotover make so little initial contact cannot be blamed on Shotover's aloofness either. He volunteers his advice to Mangan quite unexpectedly, who considers it "fairly blunt" (5,87). Later in Act I, he engages in a lengthy political discussion with Hector Hushabye in which he counsels him to distrust and resist men like Mangan. In both these cases, Shotover sets out to teach someone a lesson, establishing the fact that he has advice to give, and is not reluctant to give it to a stranger or a friend. Shaw, of course, uses this act to establish the features of Shotover's character: his blunt honesty, his ability to appraise people, and his anti-capitalist political convictions. Shotover's tendency to teach, or even preach, also emerges along with those characteristics.

Even though she may have little contact with the Captain early in the play, Ellie nevertheless learns much in the first act. As the play opens, she seems hopelessly naive. She tells Hesione,

> Mr. Mangan did an extraordinarily noble thing out of pure friendship for my father and respect for his character. He asked him how much capital he wanted, and gave it to him. (5,75)

Mangan's deed, far from being noble, was an act of cynical exploitation as we, and Ellie, later find out. Not only is she politically innocent, she is also the victim of hopeless romantic fantasies, such as the one about Desdemona:

> Don't you think it must have been a wonderful experience for Desdemona, brought up so quietly at home, to meet a man who had been out in the world doing all sorts of brave things and having terrible adventures, and yet finding something in her that made him love to sit and talk with her and tell her about them? (5,78-79)

Although Hesione tries to disabuse Ellie of these notions with argument, only Hector's revelation that his pose as Marcus Darnley has been a hoax can awaken Ellie to her own foolishness. Her response is not to be crushed by the revelation, but rather to be hardened:

> I am not damning him [i.e., Hector]; I am damning myself for being such a fool. [*Rising*] How could I let myself be taken in so? [*She begins prowling to and fro, her bloom gone, looking curiously older and harder.*] (5,84)

This "hardening" that Ellie is undergoing is deceptive, however, for Ellie is indeed "heartbroken" by her discovery that Hector is a liar. As she tells Hesione, "I have a horrible fear that my heart is broken, but that heartbreak is not like what I thought it must be." Hesione responds appropriately, "It's only life educating you, pettikins" (5,85)

That Ellie has found that heartbreak is much different than she suspected, that it leaves her hardened instead of whimpering, is an indication that she has left behind many of her romantic fantasies for a more honest realism. Moreover, it emphasizes her strength of character by portraying her as self-sufficient enough to withstand the destruction of her ideals.

Hesione's remark that "life" is educating Ellie is very apt if we recognize that when "life" educates Ellie, she is learning by herself. The story of the first stage of Ellie's education is the story of her self-education. Faced with a betrayal, her dream destroyed, she must find new depths of character and self-sufficiency. Here it becomes evident that Shaw has shifted his focus in the process of learning to the student rather than the teacher. *Heartbreak House* thus becomes a play that is more concerned with learning than with teaching.

Ellie has culminated the first part of her education as Act II begins. Just as an allusion to Shakespeare's *Othello* has shown what a sentimentalist she was at first, an allusion to *Romeo and Juliet* indicates her change to a hard-hearted kind of realism. After mentioning "engagement" to a surprised Mangan, she goes on to say,

> Mr. Mangan, we must be sensible, mustn't we? It's no use pretending that we are Romeo and Juliet. But we can get on very well together if we choose to make the best of it. (5,107)

Ellie's new realism goes hand-in-hand with an individualism into which her encounter with heartbreak has pushed her. As Mangan attempts to shock her with his story of the brutality of the business world, she mockingly says, "But it's [Mangan's story] quite interesting. Only, you must explain it to me. I don't understand it" (5,108). These words echo her first conversation with Shotover, except that now "she composes herself to listen with a combination of conscious curiosity and unconscious contempt" (5,108: stage directions). She is still genuinely curious, but no longer helplessly dependent on what others can teach her. She only wants to hear Mangan's story so she can use it for her own betterment, even if she has to use it against him. Thus her resolve to marry Mangan does not change, but her motives do. She no longer wants to show gratitude to him; she wants to make herself comfortable.

Still though, she will marry Mangan. This is the potential tragedy that looms in the play's background even more ominously than the German bombs. Allegorically, it is the sacrifice of life and youth to deadening capitalism, a fate Shaw abhors even more than war. It matters little whether the sacrifice is justified in terms of a nineteenth-century sentimentality, or more modern cynical materialism.[9] Ellie's self-education demonstrates her strength and vitality, her capacity to learn, but it fails to extricate her from what Shotover recognized immediately as an event that would shake "the stars in their courses" (5,87): her marriage to Mangan. She must be saved from this fate by learning Shotover's lesson: "your soul sticks to you if you stick to it; but the world has a way of slipping through your fingers" (5,143).

Shaw awakens a suspicion in his audience that Ellie's cynicism is a rather uncomfortable pose for her through the exchange between Ellie and Hesione later in Act II. Again the subject of Hector has been broached, and Ellie tells Hesione, "Oh, don't slop and gush and be sentimental. Dont you see that unless I can be hard—as hard as nails—I shall go mad" (5,122). Ellie's hard-headed materialism is the "something iron, something stony" (5,123) that she needs, but her strident, almost desperate, insistence on that pose belies the heartbreak that underlies it. Still she has had little contact with Shotover, but it is safe to say that their relationship begins shortly afterwards when Mangan has been almost totally broken. When Lady Utterword sees Mangan sobbing and asks what is wrong, Ellie gains Shotover's attention with this reply:

> His heart is breaking: that is all. [*The Captain appears at the pantry door, listening*]. It is a curious sensation: the sort of pain that goes mercifully beyond our powers of feeling. When your heart is broken, your boats are burned: nothing matters anymore. It is the end of happiness and the beginning of peace. (5,140)

The speech seems aimed at the Captain, not only because of the nautical image, but because it speaks to the issues in life, which he deems important. Moreover, it reveals to him Ellie's strength, understanding, and honesty—virtues that he feels the others in his house lack. He is drawn into the conversation, and, when Hector, Ariadne, and Randall rush out in conflict, he is left alone with Ellie to answer the most important question of the play, "Do you think I ought to marry Mr. Mangan?" (5,142). The process of his answering the question provides the most important exchange in the play, and Shaw's most convincing portrayal of teaching and learning. It is convincing because it transcends the mere transference of knowledge from Shotover to Ellie, becoming Shotover's personal confession.

Shotover is a reluctant teacher, advising Ellie at first that she will get "the best of the bargain" in marrying Mangan. Yet after he tells her that "if you're marrying for business, you can't be too businesslike" (5,142), he warns her against selling her soul. Ellie dismisses his advice as old-fashioned, and, again asserting her independence, tells Shotover that he cannot help her. Shotover's sharp reply, "What did you expect? A Savior, eh?" (5,145), sparks Ellie to her accusation that Shotover always draws away from sustained dialogue. Shotover can only plead confusion, then gradually reveal his dependence on rum. Yet in gradually drawing Shotover's secret from him, Ellie comes to a feeling of self-sufficiency: "I feel now as if there was nothing I could not do, because I want nothing" (5,148). Unlike Caesar or Undershaft, who attempt to impart their strength, Shotover imparts to Ellie his weakness. Yet there is a strength in weakness—his honesty in admitting it. It bespeaks a genuine personal concern in Shotover, which is lacking, or suppressed, in Caesar. More importantly, Shotover does not teach Ellie that he is weak; he lets her learn. Unlike Undershaft, who must persuade Barbara actively, Shotover passively allows himself to be used as a tool for Ellie's education. His, of course, is a controlled passivity—he responds to her, advises her, and focuses her concern—but the impulse to education comes from Ellie. Thus, Shaw successfully deals with the personal dimension of knowledge by realizing that education is the process of learning, not of teaching.

Shotover's lesson is most succinctly stated in his puzzling pronouncement, "there is no blessing on my happiness" (5,169). The play opposes "blessing" to "happiness", "self-sufficiency" to "comfort", with Ellie learning from Shotover that blessing and self-sufficiency are to be preferred. The lesson is a personal one, of course, as Ellie and Shotover's engagement indicates, but it is political as well. Ellie's opting for self-sufficiency is Shaw's ardent hope that England's newer generations will do the same. Ellie's eager anticipation of the return of the bombers is the final proof of her acceptance of political responsibility.

The play's politics remain open-ended as it closes. We have seen no glimpse of a new ruler, no vision of an ideal society. Rightly so, because Shaw's lesson is that the ideal society is not a static vision, but rather an unending process of individuals coming to terms with themselves and with others. The play's profoundest point, as seen in Ellie's relation with the Captain, is that individuals come to terms with themselves by coming to terms with others. The failure of a convincing personal relationship in *Caesar and Cleopatra*, and the neglect of personal vision in *Major Barbara*, make these plays finally less hopeful than the more superficially bleak *Heartbreak House*. Shotover is a deceptive sort of hero, and a far different one from Caesar or Undershaft, primarily because he seems to have little means to contradict the general pessimism that emerges from the play. But while he really has little to teach, in comparison with Caesar or Undershaft, he succeeds precisely because he realizes that Ellie's salvation does not lie in any social or political truth that he can impart to her, but rather in her own recognition of the potential power within her.

If self-awareness emerges from the social context of interpersonal relations, the importance of Shaw's didactic emphasis becomes clear. Art as a means to self-awareness, cannot neglect the interpersonal communication of reader and author. Much of art's power lies in the ability to multiply and extend the possibilities for human communication. To the passive reader, the communication proceeds in only one direction; thus Shaw attempts to shock the reader out of passivity with comedy, irony, and paradox, embodying these qualities in his characters, but also making his own voice felt in explaining his plays. Because he felt art had a social context, Shaw saw it his task to remind the reader that in reading, he dealt not only with art, but with an artist, and with humanity, as well. What Shaw demonstrates in the education of Ellie is that education is not the transmission of knowledge, but one mind encountering another. Our acceptance of that idea clarifies our understanding of Shaw's purposes in authorial intrusion for didactic purposes in all of his plays.

NOTES

[1] Robert Brustein, *The Theatre of Revolt* (Boston: Little, Brown, 1962), p. 183.

[2] For a discussion of the teacher-pupil relationship in Shaw's plays in terms of the Epigone-Cheiron myth, see Peter Ure, "Master and Pupil in Bernard Shaw," *Essays in Criticism*, 19 (January 1969), p. 118-139.

[3] Other of Shaw's plays, notably *Pygmalion*, also introduce the teacher-student relationship. Quotations from the plays in this essay are taken from Bernard Shaw, *Collected Plays with Their Prefaces*, ed. Dan H. Laurence (New York: Dodd, Mead, 1971), volumes 2, 3, and 5. Volume and page references to this edition follow the quotations in parentheses.

[4] Charles A. Berst, "The Anatomy of Greatness in *Caesar and Cleopatra*," Journal of English and Germanic Philology, 68 (January 1969), p. 87.

[5] Peter Ure argues that isolation from society is one of the recurring characteristics of Shaw's teacher-heroes, including Caesar (p. 118). Norbert F. O'Donell, "The Conflict of Wills in Shaw's Tragicomedy," Modern Drama, 4 (February 1962) argues that Caesar is "sympathetic but ultimately impersonal" in his attitudes toward people around him (p. 423).

[6] Brustein notes the "new mood, the new structure, and the new techniques" of the play, and argues that at this point, "Shaw is losing faith in his usual forms of revolt" (pp. 222-223). Eric Bentley sees "the end of *Heartbreak House*" as "the beginning of the later Shavian drama," and concurs with Brustein that the play is a demonstration that Shaw's earlier teachings "are all being disregarded or defeated." See Eric Bentley, *Bernard Shaw, 1856-1950* (Norfolk: New Directions, 1957), pp. 140-141.

[7] Bentley briefly notes the symbolic roles of the characters: Hesione as Love, Ariadne as Empire, Randall as Pride, Hector as Heroism, Mangan as Realism and Business, and Shotover as Aged Intellect (p. 138). Paul Hummert, *Bernard Shaw's Marxian Romance* (Lincoln: University of Nebraska Press, 1973), pp. 124-129, provides a more lengthy reading of the play as a political allegory that attacks and ultimately destroys Mangan (Capitalism).

[8] Bentley, p. 138.

[9] Shotover himself explicates the allegorical significance of Ellie's first change of character when he says, "I see my daughters and their men living foolish lives of romance and sentiment and snobbery. I see you, the younger generation, turning from their romance and sentiment and snobbery to money and comfort and hard common sense" (15, 118).

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PARTIAL DEVELOPMENT OF THE RAT TAPEWORM IN PARENTERALLY FED HOSTS

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ABSTRACT. Development of *Hymenolepis diminuta* in rats fed solely subcutaneous injections of a nutrient solution was compared with tapeworm development in similarly infected rats fed orally; parenterally fed rats had worm burdens similar to those of normally fed animals at 7 days postinfection, but few hymenolepids were recovered from parenterally fed hosts at 10 days postinfection. Tapeworms from orally fed animals were consistently larger and of greater mass than those from the parenterally fed rats. Excystation and some development of *H. diminuta* in parenterally fed rats (infected *per os* with cysticercoids) is described.

INTRODUCTION

A recent study indicates that rats subjected to long term intravenous feeding will support the development of the mucosal-dwelling nematode *Trichinella spiralis*, but not that of the lumen-dwelling cestode *Hymenolepis diminuta* (Castro et al., 1974). Because *H. diminuta* incorporates intravenously injected lipid precursors (Kilejian et al., 1968), subcutaneously injected B vitamins (Platzer & Roberts, 1969), and also assimilates material from the exocrinoenteric circulation (Read, 1950; Read and Simmons, 1963), further studies of tapeworm development in parenterally fed rats were initiated in an attempt to resolve this seeming discrepancy.

Castro et al. (1974), in discussing the failure of *H. diminuta* to develop in their parenterally fed animals, noted that nondietary factors (such as bile composition) were critical to the maturation of cestodes. Since the role of bile salts in excystation is well established (MacInnis and Voge, 1970), the present study was undertaken to examine specifically the development of *in vitro*-excysted *H. diminuta* cysticercoids (which had been surgically implanted in the duodenum) in rats receiving parenteral nutrition by a subcutaneous (subQ) route. In addition, comparisons were made between parenterally (subQ) and orally fed rats that had been infected traditionally *per os* with cysticercoids.

MATERIALS AND METHODS

Mature (500+ g), conventionally bred, male Sprague-Dawley rats were used in this study. They were weighed initially and placed in separate cages. Rats designated as controls were maintained on lab chow and water *ad libitum*. Experimental rats received water *ad libitum* and subcutaneous injections of a sterile cell culture medium (RPMI #1640, Gibco, Grand Island, New

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York; powdered reagents were dissolved in one liter of 40% dextrose instead of distilled water). Subcutaneous delivery of quantities of fluid is a common clinical practice in newborn infants (Harvie, 1962; Ziai, Janeway & Cooke, 1975) where intravenous administrations might be contraindicated. Consequently, this simpler method of parenteric feeding was used instead of harnessing animals that had surgically implanted, chronic intravenous catheters, as employed by Castro et al. (1974, 1976). In the present study two or three daily injections of this medium (which contained salts, essential amino acids, and vitamins) into the dorsal subcutaneous connective tissue were used to deliver 20-30 ml/rat each day. After subcutaneous feedings were initiated (2-3 days), both control (orally fed) and experimental rats were each infected with 20 *H. diminuta* cysticercoids under light ether anesthesia. Artificial excystment was performed as described by Roberts (1961), and in these animals infections were initiated by intraduodenal implantation through an 18-gauge needle to the surgically exposed small intestine. Other parenterally nourished and orally fed rats under mild ether anesthesia were infected with 20 cysticercoids by esophageal intubation. MacInnis and Voge (1970) described the methods used for rearing and infecting the intermediate host and collection of cysticercoids, as well as perfusion of adult tapeworms from infected rats. At 7-14 days postinfection the rats were reweighed and killed; tapeworms were removed by perfusing the small intestine with Ringer's saline. The perfusate was carefully examined with a dissecting microscope and the worms removed, rinsed twice in saline, and stored in 70% ethanol overnight. Each small intestine was also slit longitudinally and microscopically examined, but in all instances worms were recovered only from the perfusate. The tapeworms were removed from the ethanol solution to heat-dried, tared containers. One day later they were placed in a 60° C-oven and three days later, ethanol-extracted dry weights were determined. Some ethanol-fixed worms were stained with aqueous celestine blue (Riser, 1949) and wholemounts routinely prepared for microscopic examination.

RESULTS

Tapeworms were recovered 7 days postinfection from subcutaneously (parenterally) fed rats that had been infected surgically with *in vitro*-excysted cysticercoids; subcutaneously fed rats that had been routinely infected with untreated cysticercoids also harbored worms at 7 days postinfection (Table 1). The role of bile salts in the development of *H. diminuta* has been established (Goodchild, 1958). The present study suggests no relationship between parenteral (subQ) feeding and nonexcystment of cysticercoids, as well as implying that sufficient bile is present in these rats for at least limited initial development (0-7 days) of this tapeworm.

Further studies compared development of this cestode 7-14 days postinfection in normally and parenterally fed animals (Table 1). Similar worm burdens of *H. diminuta* were recovered from parenterally and normally fed animals 7 days postinfection. In the subcutaneously fed rats only two of the three surviving animals were parasitized (1 tapeworm/rat) at 10 days postinfection, and no tapeworms were recovered from this experimental group 12 or 14 days postinfection. Hymenolepids recovered from normally fed animals were consistently much larger and had greater mass than the tapeworms from parenterally fed animals.

Microscopic examination of 7- and 10-day-old tapeworms indicated that the ethanol-fixed specimens were in varying states of contraction, so measurement of total lengths was not attempted. Examination of the proglottids indicated that the maturation of tapeworms from orally fed control rats corresponded to previously described patterns (Roberts, 1961). Seven days postinfection, segmentation and prominent lobate ovaries were obvious; vitellaria, seminal receptacles, and cirri could also be identified in many segments. In contrast, cestodes from subcutaneously fed rats were not maturing in a normal manner. Tapeworms were obviously segmented at 7 days postinfection but the only genital primordia easily recognized corresponded to a nonlobed ovarian mass. (This stage approximates 5-day development described by Roberts (1961) in normal animals.) At 10 days postinfection, developing ova were observed in uteri of the terminal proglottids of tapeworms from orally fed rats; both the ovaries and testes appeared to be degenerating in these terminal proglottids. Ten-day-old worms from parenterally fed rats were segmented and in some proglottids a lobate ovarian mass was observed. Comparison of 7- and 10-day-old hymenolepids from parenterally fed rats suggested that little maturation occurred during these intermittent three days.

Table 1. Development of *Hymenolepis diminuta* in parenterally and normally fed rats

	Worm Age (Days)	Parenterally Fed: Number of Worms Recovered	Parenterally Fed: Total Dry Weight (mg)	Parenterally Fed: Mean Weight per Worm (mg)	Enterically Fed: Number of Worms Recovered	Enterically Fed: Total Dry Weight (mg)+	Enterically Fed: Mean Weight per Worm (mg)
	7	6[°]	1.1	0.18	—	—	—
	7	4[°]	1.1	0.27	—	—	—
	7	10	2.3	0.23	—	—	—
	7	11[a]	n.d.	n.d.	—	—	—
	7	5	1.4	0.28	6	6.7	1.11
	7	11	2.0	0.18	9	7.1	0.79
	7	17	3.5	0.20	20	36.6	1.83
7-Day	Mean ± S.D.			0.223 ± 0.044**			1.243 ± 0.533
	10	1	0.5	0.5	1	8.2	8.20
	10	1	0.4	0.4	15	278.3	18.55
	10	0?[a]	—	—	13	292.7	22.51
10-Day	Mean ± S.D.			0.450			
	12	0	—	—			16.420 ± 7.389
	12	0	—	—	16	451.3	28.14
	14	0	—	—	17	573.8	33.79
	14	0	—	—	16	810.8	50.67
	14	0	—	—	8	316.3	39.47
14-Day	Mean ± S.D.			—	18	1020.5	56.74
							48.960 ± 8.761

+ Ethanol-extracted dry weight
** $P < 0.001$, 't'-test.
[°]Rats infected with *in vitro*-excysted cystercercoids; [a] Rat autopsied 1-5 hours post-mortem, n.d. = not determined.

Body weights (Means ± S. D.), monitored for comparative purposes, indicated that subcutaneously fed, parasitized rats lost an average of 58.01 ± 44.59 g (a 13.06% Initial Body Weight (= IBW) reduction) in the first 7 days, and an average of 154.37 ± 8.42 g (-27.59% IBW) during the first 10 days postinfection. Parasitized control animals lost 24.21 ± 3.24 g (-3.80% IBW) in days 0-7, 31.33 ± 5.03 g (-5.04% IBW) in days 0-10, 32.67 ± 4.04 g (-5.30% IBW) in days 0-12, and 37.75 ± 3.68 g (-6.16% IBW) in days 0-14. A separate group of nonparasitized subcutaneously fed controls lost 10.12% IBW 7 days after sham infection and 18.62% IBW at 10 days. This loss suggests the possible influence of stress, or malnutritive factors, or both associated with subcutaneous feeding in these older rats.

DISCUSSION

The growth and maturational requirement of *H. diminuta* for bile salts has been established by Goodchild (1958). Although concentrations of bile salts were not measured, the present study implies that sufficient quantities of bile salts are present in the intestines of (subQ) parenterally fed rats to permit at least limited initial development of this tapeworm.

Cestodes develop in parenterally fed rats during the first 7 days postinfection, but are completely lost from the intestines of subcutaneously (the present study) or intravenously nourished (Castro et al., 1974) rats by 14 days postinfection. These observations may be related to changes in carbohydrate utilization that occur during the period from 7 to 14 days postinfection. *H. diminuta* and the rat host compete for ingested nutrients; Mettrick (1973) suggested that up to 50% of the ingested carbohydrate may be absorbed by these tapeworms. Other studies indicate that the development of *H. diminuta* is impaired in rats maintained on a carbohydrate deficient diet (Chandler, 1943; Read and Rothman, 1957; Read, 1959). Data from Roberts' (1961) studies indicate that in 10-worm populations of *H. diminuta* the total carbohydrate (= CHO) concentration increases from 0.25 mg dry weight CHO per worm at 7 days postinfection to 7.99 mg CHO at 10 days and 32.3 mg CHO (a 120-fold increase) at 14 days postinfection. In 20 worm populations total carbohydrate similarly increased 30-fold during the period from 7-14 days postinfection (Roberts, 1961). *In vitro* studies indicate that additional glucose must be supplied to *H. diminuta* at 8 and 10 days in order to culture this tapeworm in the laboratory (Schiller, 1965). That this critical period of development (7-14 days postinfection) exists is further supported by the results of the present study taken in conjunction with the observation that tapeworms from rats fed orally for 16 days, then switched to intravenous feeding will initially destrobilate, then continue to develop, but have lesser mass (Castro et al., 1976).

Read and Rothman (1957) observed an almost complete cessation of egg production by *H. diminuta* when hosts were subjected to a carbohydrate deficient diet, and suggested that ovarian function might be directly affected by the available dietary carbohydrate. In perhaps a similar manner, the seeming delay in ovarian and proglottid maturation seen in the present study of strobila from parenterally fed rats might be tentatively attributed to a deficiency in the availability of carbohydrates or other essential compounds. Furthermore, the destrobilization of tapeworms from rats fed enterally for 16 days occurred after hosts were switched to intravenous feeding (Castro et al., 1976).

In reviewing the role of carbohydrate in the growth of *H. diminuta* and other cestodes, Read (1959) noted that the higher the growth rate, the greater is the sensitivity to a lack of carbohydrate in the host diet. Another factor must therefore be considered in relation to the results of the present study. Namely, a 6- (10-worm populations) to 20-fold (20-worm populations) increase in dry weight occurs between 7 and 10 days postinfection, but there is only a 2-3 fold increase in length during this time (Roberts, 1961). Since surface area is a function of length, and weight a function of tapeworm protoplasm, a decrease in the ratio of absorptive surface area to protoplasm (S. A./P) probably occurs between 7-10 days postinfection. This phenomenon may contribute to the seeming failure of tapeworms to survive in parenterally fed rats. The possibility that in normally fed animals the tapeworm might compensate for changes in the S. A./P ratio by kinetically altering or initiating functional operation of mediated, active transport mechanisms (Read et al., 1963) during this period is a speculation that warrants further study.

The considerable weight reductions and loss of two parasitized animals confirms that the (subQ) parenterally fed rats provided a less than optimal environment for the development of intestinal tapeworms. This, however, does not explain the failure of the rat tapeworm to develop beyond 10 days postinfection, since intravenously fed rats, which showed positive weight gains during the experimental period, also failed to support development of this tapeworm (Castro et al., 1974). Weight losses associated with *H. diminuta* infections, as seen among orally fed rats in the present study, are not uncommon (Mettrick, 1972) and may be attributed to the sensitivity of older, large animals to pathophysiological changes described by Podesta and Mettrick (1974).

Thus, although *H. diminuta* is highly successful in competing for ingested carbohydrates (Mettrick, 1973) and capable of assimilating nutrients from the circulatory system of the host (Chandler et al., 1950; Kilejian et al., 1968; Platzer and Roberts, 1969; Castro et al., 1976; the present study), growth-associated changes in the energy or nutritional requirements during the second week postinfection seem to be responsible for failure of this tapeworm to survive in parenterally fed rats.

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